ECOPHYSIOLOGICAL BASES FOR THE DISTRIBUTION OF RAINFOREST AND EUCALYPT FOREST IN SOUTHEASTERN AUSTRALIA.

by

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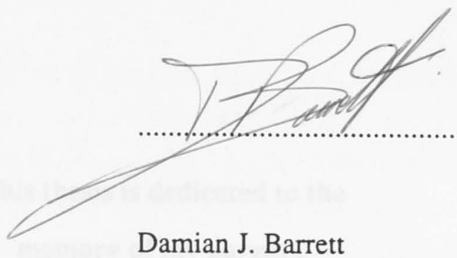
STATEMENT OF ORIGINALITY

The work presented in this thesis is my own. Specific contributions by others are referred to in the text and acknowledgements.



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This thesis is dedicated to the

memory of my parents,

John and Margaret.

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ABSTRACT

In mountainous terrain in southeastern Australia, rainforest vegetation is associated with gully bottoms and south facing (sheltered) aspects, whereas eucalypt forest occurs on north facing (exposed) aspects and ridge tops. The principal environmental factors which vary in association with rainforest and eucalypt forest distribution are light and soil moisture. Exposed aspects and ridge tops may receive higher irradiance and may have lower soil moisture content than sheltered aspects. Consequently, interactions between plant growth and water use with variation in irradiance and soil moisture may be an important determinant of vegetation distribution. The aim of this thesis is to understand how plant responses to variation in microenvironment are related to the differential distribution of vegetation types with aspect.

In two glasshouse experiments, seedling growth, biomass partitioning and water use characteristics were studied under different light and water treatments in representative canopy species from rainforest and eucalypt forest. Growth responded primarily to light treatments and was greatest in eucalypt species at light levels greater than 20% sunlight (approximately 430 μmol photons m^{-2} s^{-1}). However, biomass was greatest in rainforest species at light levels below 20% sunlight. Leaf area ratio increased and specific leaf weight decreased in eucalypts at less than 28% sunlight, but did not vary significantly between light treatments in rainforest species. When soil moisture was abundant, transpiration rates per unit leaf area were not different between rainforest and eucalypt forest species. An increase in leaf area at high irradiance in all species was associated with a porportional increase in root mass, but was not associated with an increase in water uptake rate. Thus, similar transpiration rates may have partly been due to biomass partitioning between water uptake (root) and water loss (leaf) structures in response to water and light treatments. Fast growth rates, greater morphological plasticity, and a more ramified and finer root system in eucalypt seedlings are characterisitics which may be advantageous to growth and survival under high irradiance and low water availability such as occur on exposed aspects. Alternatively, slower growth rates, shallow and less ramified

root systems in rainforest species may be deleterious to growth and survival in dry, exposed sites. Under low light treatments (80-130 μmol photons m^{-2} s^{-1}) biomass gain was higher in rainforest species than eucalypts. High growth rates under low irradiance may enhance survival under low light conditions which occur on sheltered aspects during winter and beneath the rainforest canopy.

In a forested catchment in southeastern New South Wales, field studies were conducted to quantify canopy structure, tree size, crown area and water use characteristics of the dominant rainforest and euclaypt forest trees on four experimental plots situated in the gully bottom and upslope on both exposed and sheltered aspects. Canopy leaf area index, estimated using hemispherical photographic techniques, was higher in rainforest than in eucalypt forest plots and was greater in summer than in winter or autumn, presumably because of seasonal variation in canopy leaf area. Eucalypt forest plots were characterised by relatively large trees of greater biomass and larger crown area. Rainforest plots, however, had characteristically smaller trees of lower biomass and smaller crown area.

On each experimental plot, canopy transpiration and conductance to water vapour were estimated in eight trees from measurements of sap flow, crown area, atmospheric humidity and canopy temperature. Previous validation experiments in saplings of rainforest and eucalypt species, had demonstrated that sap flow measurements using the heat pulse velocity technique were comparable to similar measurements from water uptake by a potometer at both high flow rates and when summed over 24 hours. Mean maximum sap flow in canopy trees *in situ* was linearly related to sapwood area in both rainforest and eucalypt forest plots. However, lower sapwood area for a given maximum sap flow in eucalypt forest trees indicated a possible lower internal resistance to water transport through xylem vessels. Mean maximum canopy transpiration rates per unit crown area in all seasons, were higher in rainforest at the gully bottom than in upslope plots of either rainforest or eucalypt forest. This was attributed to greater water availability at the gully bottom due to downslope lateral soil drainage. However, high transpiration rates in trees at the gully bottom in summer occurred when soil water was less abundant. These high

rates of transpiration may have been due to a higher leaf area index and greater canopy to air vapour pressure difference caused by increased light interception by more horizontally orientated leaves. On slopes above the gully bottom, mean maximum transpiration rates were not different between rainforest and eucalypt forest, and were not related to leaf area index, maximum midday global irradiance or soil moisture content at depths above 0.35 m in each plot.

Mean maximum canopy conductance per unit crown area decreased with decreasing humidity possibly due to stomatal closure. The "average" leaf conductance to water vapour in rainforest and eucalypt forest plots, determined from the ratio of canopy conductance per unit crown area and leaf area index, decreased linearly with increasing saturation deficit and were similar between rainforest and euclaypt forest plots. These results were consistent with a strong coupling between atmospheric humidity and canopy conductance to water vapour in rainforest and eucalypt forest canopies. Thus growth and water use characteristics in rainforest and eucalypt forest trees of southeastern New South Wales, may be strongly coupled to regional variation in climate, in contrast to growth and water use at the seedling scale which may be more dependent on microenvironment.

It was concluded that the differential distribution of rainforest and eucalypt forest with aspect in eastern temperate Australia, appears to be determined by (a) the influence of aspect, topography and overstorey canopy structure on microenvironment at the ground surface, (b) different responses by rainforest and eucalypt seedlings to variation in microenvironment, and (c) the feedback effect of canopy structure on both understorey microenvironment and fire behaviour.

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Chapter 1.

Rainforest and eucalypt forest distribution in temperate eastern Australia in relation to aspect.

Introduction

The aims of this thesis are to understand how rainforest and eucalypt forest tree species respond to variation in microenvironment and to relate these plant responses to the distribution of rainforest and eucalypt forest in eastern temperate Australia. Emphasis has been given to understanding how plant growth and water use in rainforest and eucalypt forest species from southeastern New South Wales relate to vegetation distribution patterns with aspect. Irradiance and soil moisture are the principal environmental factors which vary in relation to aspect in mountainous terrain. Consequently, laboratory studies at the scale of seedlings and field studies at the scale of adult trees were conducted to investigate interactions between plant growth and water use with variation in irradiance and soil moisture. Experimental results were used to examine the hypothesis that the distribution of rainforest and eucalypt forest is the product of plant responses to aspect mediated variation in microenvironment.

Throughout this thesis, the terms 'exposed' and 'sheltered' are used to distinguish between northerly and southerly facing slopes in order to avoid confusion resulting from different solar azimuths between southern and northern hemispheres. These terms reflect the relative amount of total annual irradiance on a sloping surface for a given angle and orientation.

This chapter contains a review of the literature on (a) the distribution of rainforest and eucalypt forest in Australia, (b) the role of fire in rainforest and eucalypt distribution, and (c) processes controlling plant growth and vegetation distribution patterns in relation to variation in aspect. Finally, the chapter conludes with an outline of the aims, hypotheses and research strategy adopted for the thesis.

The origin and distribution of temperate eucalypt forest and rainforest in eastern Australia.

Rainforest communities world-wide occupy approximately 5% of the total land surface area, yet they probably contain at least half of the world's terrestrial species of flora and fauna (Grainger 1980). Rainforests occupy an even smaller proportion (<1%) of the land surface of the Australian continent (Webb and Tracey 1981). Australian rainforests contain biota which have affinities to species on other land masses that once comprised the Gondwanan continent (Webb and Tracey 1981; Winter *et al.* 1987). Leaf fossil evidence (eg. Christophel and Blackburn 1978; Christophel 1981; Hill 1982; Barrett 1987; Barrett and Christophel 1988) shows that much of southern and eastern Australia was dominated by relatively diverse notophyll forests during the Early and Mid-Tertiary, from 65 to 30 million years ago. These Gondwanan forests have taxonomic affinities with tropical and subtropical rainforests in present day eastern Australia. The palaeoenvironment of southern Australia during the Early Tertiary was wetter than present, with less seasonality in rainfall and temperature (Kemp 1981). Increased aridity and seasonality of climate in the Late Tertiary (Kemp 1981; Specht 1981) 30 - 1.8 million years ago, resulted in the evolution of the Australian sclerophyll flora, the forests of which are dominated by *Eucalyptus* (Pryor and Johnson 1981; Kemp 1981; Singh 1982; Holmes *et al.* 1983). As the climate became more arid, rainforest became restricted to within 100 km of the eastern coast of Australia (Walker and Singh 1981).

During the Quaternary period (1.8 million years ago to present), the climate fluctuated between relatively warm, wet periods and cool, dry periods. The fossil pollen record from both northern Queensland (Kershaw 1978 and 1985) and southeastern Australia (Singh *et al.* 1981) indicates migration and change in species composition of plant communities in association with climatic fluctuations. Rainforest expansion during periods of high rainfall emanated from "refugia" or sites favourable to rainforest

persistence during relatively arid periods (Webb and Tracey 1981; Haffer 1982). Recent studies using radiocarbon dating of charcoal fragments in northern Queensland (Hopkins *et al.* 1990 and 1992), indicate the spatial extent of sclerophyll migration into most areas occupied at present by rainforest. These studies corroborate palynological evidence (Kershaw 1978 and 1985) of vegetation migration associated with climatic fluctuations over the last 34000 years.

The current distribution of sub-tropical and warm temperate rainforest vegetation in Australia is confined to a series of discontinuous patches along the eastern coast (Webb and Tracey 1981; Helman 1987; Floyd 1987; Young and MacDonald 1987). These patches are composed of species "sifted" by climate from the previously more widely distributed ancestral rainforest vegetation (Baur 1957; Webb *et al.* 1984; Read and Hill 1989). As implied by its name, rainforest occupies regions of relatively high rainfall (Baur 1957). The minimum rainfall supporting rainforest is 800 mm in tropical regions (Webb and Tracey 1980; Winter *et al.* 1987) and 1000 mm at higher latitudes. However, local variation in topography, climate and edaphic factors results in both fragmented distribution and spatial variation in structure and species composition of Australian rainforests (Webb *et al.* 1984).

Australian rainforest communities, under conditions of high moisture, warm temperatures and abundant nutrients, are characterised by a dense canopy formed from closely spaced trees on which occur epiphytes, lianes or vines (Webb and Tracey 1981). On relatively fertile sites of adequate soil moisture at relatively low latitudes and altitudes, rainforest is floristically rich and structurally complex. With increasing aridity and decreasing mean annual temperature, rainforest communities become less diverse and structurally simple (Webb and Tracey 1981; Winter *et al.* 1987). Rainforests between 29^{o} and 38^{o} latitude were characterised by Webb *et al.* (1984) as temperate or subtropical humid evergreen rainforests, possessing lower structural complexity and lower species diversity than rainforests of tropical Australia. On

mesotrophic soils, more structurally complex notophyll vine forests develop, dominated by *Doryphora sassafras, Cryptocarya glaucescens, Ceratopetalum apetalum, Schizomeria ovata* and *Dendrocnide excelsa* (Webb *et al.* 1984).

Earlier work by Beadle (1954 and 1962) on rainforest in New South Wales emphasised the importance of soil nutrient content, in particular phosphorous, in determining the distribution of rainforest and eucalypt forest in eastern Australia. Transplant experiments by Beadle demonstrated that rainforest species produced lower biomass on nutrient deficient sandstone soils, and that growth could be enhanced by the addition of fertiliser. Further work by Baur (1957), Florence (1964) and Webb (1968) also suggested that soil nutrient level and in particular soil phosphorus, were important determinants of rainforest distribution in eastern Australia. However, Tracey (1969), concluded from an extensive survey of 49 rainforest and sclerophyll sites that "ecological factors" including water supply, soil aeration and nutrients were at least as important as soil phosphorus in determining rainforest distribution.

Previous studies of aspect related distribution of temperate rainforest and eucalypt forest in eastern Australia have alluded to the relationships between microenvironment and seedling survival (McLuckie and Petrie 1927; Fraser and Vickery 1938; Burges and Johnston 1953; Baur 1957; Florence 1964; Young and MacDonald 1987). However, few studies have attempted to quantify species differences in plant responses to variation in light and soil moisture in relation to forest distribution patterns. McLuckie and Petrie (1927) were perhaps the first to have investigated differences in leaf morphology and root structure and the distribution of rainforest and eucalypt species along natural gradients of light and moisture in the Blue Mountains, New South Wales. They suggested that the distribution of each forest type was determined by the interaction between "edaphic water supply" and differences in plant morphology. Rainforest species possess leaves lacking features which restrict excessive water loss and shallow root systems which may limit water supply (McLuckie and Petrie 1927).

These features were suggested to limit establishment of rainforest species on relatively xeric sites (Fig. 1.1). Conversely, eucalypt forest species were possibly excluded from mesic sites by competition for light with rainforest species. Fraser and Vickery (1938), made similar conclusions about vegetation distribution patterns at Barrington Tops in northeastern New South Wales. Warm temperate rainforest vegetation was confined to water courses and shaded aspects in valleys where the lowest irradiances were observed, wheras eucalypt forest occurred on ridges and upper slopes which were characterised by low humidity and high irradiance (Fraser and Vickery 1938). Both Burges and Johnston (1953) and Turner (1976) attributed similar patterns of rainforest-eucalypt forest distribution in northeastern New South Wales to either fire regime or localised variation in soil moisture and nutrient content. Yates (1989) demonstrated that the probability of rainforest occurrence on any site in southeastern New South Wales decreased with increasing irradiance. This result was attributed to either limited establishment by rainforest species under high irradiance or the role of irradiance in determining fire frequency and intensity. While past studies allude to the association between rainforest and eucalypt forest distribution patterns and variation in environment with aspect, none since the pioneering work of McLuckie and Petrie (1927) and the more recent study of Yates (1989) have attempted to interpret the distribution patterns in terms of plant physiological responses to variation in water and light availability.

The role of fire in rainforest-eucalypt forest distribution in eastern Australia.

Fire is a dominant feature of Australian sclerophyll vegetation and triggers flowering and seed germination in many species (Gill 1975; Shea *et al.* 1981; Ashton 1981a). Additionally, many eucalypt species have evolved vegetative features which render them relatively fire insensitive (Beadle 1940). Thick bark in many eucalypt species imparts some resistance to fire by maintaining sub-lethal cambial temperatures during

fires (Martin 1963; Vines 1968; Gill and Ashton 1968; Gill 1975). While seedlings of both eucalypt and rainforest species are susceptible to fire, as size increases so does protection of the cambium tissues by increasing bark thickness. Additionally, epicormic buds are an adaptive feature of eucalypts which permit vegetative regrowth following crown removal by fire (Cremer 1972). From the sapling stage, many rainforest species, particularly of the ecotone, possess some degree of fire resilience by coppicing from burnt stumps and root stocks (Stocker 1981; Unwin *et al.* 1985; Ashton and Frankenberg 1976; Helman 1983; Yates 1989; Chesterfield *et al.* 1991). However, fires may enter rainforest and kill understorey and canopy trees during severe drought (Ridley and Gardiner 1961) and following extensive damage, such as from cyclones and logging (Stocker and Mott 1981).

The role of fire in controlling the distribution of rainforest and eucalypt vegetation in Australia has been emphasised in many works (Domin 1911; Burges and Johnston 1953; Cremer 1960; Jackson 1968; Webb 1968; Turner 1976; Noble and Slatyer 1980; Webb and Tracey 1981; Smith and Guyer 1983; Unwin *et al.* 1985; Stocker and Unwin 1986; Ash 1988; Unwin 1989a and 1989b; Hopkins *et al.* 1990; Chesterfield *et al.* 1991; Hopkins *et al.* 1992). It is the general consensus of these reports that, throughout eastern Australia, any amelioration of fire frequency and intensity will allow an advance by rainforest vegetation into eucalypt forest. Alternatively, as fire frequency increases, a "mutual causal cycle" favours the development of pyrophytic vegetation, preventing invasion by rainforest species (DeAngelis *et al.* 1986). Indeed, Mutch (1970) proposed the hypothesis that fire dependent plant communities have higher fire frequencies because of selection for flammable characteristics. Jackson (1968) formalised the "fire-control hypothesis" for cool temperate wet sclerophyll forests and rainforests of Tasmania in regions receiving >600 mm rainfall annually. In his model, the variable governing vegetation dynamics was the time interval between fires. A fire event was stochastic, but the probability of fire within a given time period was higher in pyrophytic than pyrophobic communities. Jackson suggested that succession from

"mixed forest" (consisting of eucalypt overstorey above a rainforest canopy) to pure rainforest occured when a fire disturbance interval exceeded the regeneration time of eucalypt species, generally greater than 250 years. More frequent fires resulted in the establishment of successively more pyrophytic vegetation until, at fire frequencies of less than 20 years, grassland and sedge communities were dominant. Noble and Slatyer (1981) developed a model based on Henderson and Wilkins' (1975) estimates of the proportion of area occupied by different vegetation types under Jackson's (1968) estimated fire frequencies for different vegetation types. This model predicts that if fire was completely eliminated from all sites, rainforest vegetation would eventually exclude eucalypt forest species in high rainfall regions as shown in Fig. 1.2. However, prior to development of the "fire control hypothesis" Florence (1964) contended that fire had little impact on the distribution of rainforest and eucalypt forest at temperate latitudes in Australia, suggesting instead that soil moisture and nutrient contents were of greater influence. Additionally, Unwin (1989a) and Ash (1988) emphasised the importance of interactions between many environmental factors, including soil mositure and nutrients, in controlling rainforest-eucalypt forest boundary dynamics in northeastern Queensland.

Fire frequency, intensity and behaviour vary between climatic regions in Australia (Gill 1975). Frequent, low intensity grass fires are characteristic of northern Australia (Webb and Tracey 1980; Stocker and Mott 1981), whereas, infrequent very high intensity crown fires are more characteristic of southeastern Australia (Gill 1975; Ashton 1981a; Gill 1981). Topography also influences fire behaviour through slope angle and aspect (Luke and McArthur 1978; Cheney 1981; Walker 1981). Fire intensity and rate of spread increase with increasing slope angle, wind speed, fine fuel fraction, fuel load, flammibility and fuel moisture content (Luke and McArthur 1978). Fuel moisture content is generally lower on exposed aspects and consequently fires are of greater intensity than on sheltered aspects (Cheney 1981). Additionally, eucalypt forests maintain higher fuel loads (Walker 1981) than rainforest vegetation. Yates

(1989) showed that fine fuel fraction in eucalypt forest of southeastern New South Wales was twice that of adjacent rainforest. As a consequence, rates of spread and intensity of fires tend to be greater on exposed than shaded aspects (Fig 1.3; Cheney 1981) and tend to be greater in eucalypt forest than in rainforest.

Well defined boundaries between rainforest and eucalypt vegetation are observed in locations subject to frequent fires, with boundaries becoming more diffuse with less frequent burning (Webb 1968; Ash 1988). The abruptness of the boundary results from the fire resistant nature of the rainforest ecotone (Unwin 1989a). Thus, in rugged terrain typical of many parts of eastern Australia, sharply defined rainforest-eucalypt forest boundaries may be expected on exposed aspects where fire intensity is maximum. More diffuse boundaries may be expected on shaded aspects when fire intensities are lower. Indeed, these observations have been made by Yates (1989) in southeastern New South Wales. In this region, evidence of fire is found in both rainforest and eucalypt vegetation types, although fire intensity as indicated by trunk scorch height and fire scars, is greater in eucalypt forest on exposed aspects, than in rainforest on sheltered aspects and gully bottoms (Yates 1989, and personal observation).

A quantitative investigation of the role of fire in controlling the dynamics of the rainforest-eucalypt forest boundary is beyond the scope of this thesis. However, inferences as to its impact on vegetation distribution patterns may be made on the basis of published literature. Fire is an important component of Australian forest systems, but it would be erroneous to regard fire as an external factor imposed on plant communities and controlling their distribution. Fire frequency and intensity are strongly dependent on site microenvironment, topography and vegetation type. In this way fire, is a process which has a positive feedback on vegetation dynamics. Thus, fire in rainforest and eucalypt forests of southeastern New South Wales may be regarded as a mechanism which (a) reinforces distribution patterns initiated by plant responses to

light, water and nutrients, and (b) determines the dynamics and abruptness of rainforest ecotones.

Aspect mediated distribution of plant communities.

(a) Vegetation distribution in relation to microenvironment.

The influence of aspect on microclimate and vegetation distribution has been studied for over 140 years. Ludwig *et al.* (1957), Cantlon (1953) and Lundqvist (1968) cite papers by Snedtner (1854) and De Candolle (1855) who documented differences in vegetation with aspect in the European Alps. Later, Turesson (1914), who investigated the association between *Pseudotsuga menzeisii* and shaded aspects in semi-arid regions of northwestern United States, stated:

> "It is a well-known fact that vegetation of hills and mountain slopes differ according to the exposure of the locality to different quarters of the compass."

Subsequently, many studies have described the association between plant distribution, variation in microenvironment and aspect. Published results from twenty-one experimental studies which specifically investigated both microclimate and plant ecology in mountainous terrain from 1914 to 1991 are summarised in Table 1.1. In all studies of microclimate, soil and air temperatures were greater, and soil and atmospheric moisture contents were lower on exposed than on sheltered aspects. Only one study demonstrated no difference in soil moisture between aspects; this result was attributed to seepage from the water table (Feldhake and Boyer 1990). In all studies on aspect related plant ecology, species diversity, stem frequency and stem basal area were mostly greater on sheltered than on exposed aspects. These studies have established an

association between aspect mediated variation in irradiance, soil moisture content, evaporation and temperature of soil and air with plant growth and patterns of vegetation distribution in the natural environment. Consequently, rainforest and eucalypt vegetation distribution patterns in eastern Australia may also be related to species differences in plant growth in relation to variation in microenvironment with aspect.

(b) The influence of topography on ground surface irradiance.

Variation in microenvironment between exposed and sheltered aspects (Table 1.1) is due to the effect of topography on ground surface irradiance. On a sloping surface, the global irradiance, I_g, on a clear day is determined by the quantity of particulate matter and the gaseous composition of the atmosphere, the solar beam path length and the azimuth and slope angle of the receiving surface (Lee and Baumgartner 1966; Garnier and Ohmura 1968; Swift 1976; Gates 1980; Flint and Childs 1987; Jones 1992; Rowland and Moore 1992). Global irradiance is calculated as,

$$I_g = I_S \tau^m \cos i + I_d \qquad (1.1)$$

where I_S is the solar constant and is equal to 1367 J m^{-2} s^{-1} (Gates 1980; Nobel 1991; Jones 1992) although it may vary by up to 3.5% with season due to non-circularity of the earths orbit, and τ is the atmospheric transmissivity which is a function of scattering of light by particulate matter and absorption by atmospheric gases. Depending on atmospheric conditions τ may vary between 0.6 and 0.8 (Gates 1980). The path length, *m*, of the direct solar beam through the atmosphere is equal to secant θ, where θ is the solar beam zenith angle (Gates 1980; Nobel 1991; Jones 1992). The diffuse radiation, I_d, is approximately a constant fraction of I_g for a given atmospheric transmissivity (Jones 1992) and is caused by scattering of light in the atmosphere. For values of τ between 0.6 and 0.8, I_d varies between 0.4 and 0.2 of I_g (Jones 1992). The angle, *i*, is

that between the beam direction and a normal perpendicular to the receiving surface (Gates 1980; Jones 1992) and,

$$\cos i = [(\sin \phi \cos h)(-\cos \alpha \sin \theta_S) - \sin h (\sin \alpha \sin \theta_S) + (\cos \phi \cos h)] \cos \delta + [\cos \phi (\cos \alpha \sin \theta_S) + \sin \phi \cos \theta_S] \sin \delta \quad (1.2)$$

where ϕ is the site latitude, h is the angular distance of the sun from the meridian, α is the surface aspect, θ_S is the zenith angle of a normal to the surface and δ is the solar declination for any time of the year.

Cos *i*, and therefore global irradiance at the ground surface, is dependent on slope angle, aspect and season (Fig. 1.4). In mountainous terrain at 35° 30' latitude, maximum direct beam irradiance during midday in summer would be observed on slope angles between 10 and 15° on exposed aspects. Irradiance decreases with increasing slope angle between 15° and 90° during summer (Fig. 1.4). Maximum irradiance in winter, however, would be observed on slope angles between 55 and 60° on exposed aspects. On shaded aspects in winter, irradiance decreases rapidly with increasing slope angle up to approximately 30°, beyond which the ground surface would be in continuous shade. As a consequence of the relationship between aspect, slope angle and irradiance, there is variation with aspect in energy dependant processes such as soil evaporation, ground surface temperature and atmospheric humidity (Hutchins *et al.* 1976; Radcliffe 1982; Tajchman and Lacey 1986; Feldhake and Boyer 1990). Thus, in mountainous terrain, environmental gradients of light and soil moisture result from the interaction between irradiance and topography. Interactions between micronevironment and plant genotype are manifest in plant growth, and differences in plant growth and water use characteristics in relation to microenvironment may underlie vegetation distribution patterns.

(c) Plant growth and water use along light and water gradients.

At the seedling scale, rates of plant growth are, in part, determined by the interaction between genotype and resource availability (Hunt and Lloyd 1987; Hunt 1990). High growth rates may increase plant size which may further enhance resource acquisition (Grime and Hunt 1975; Goldberg and Werner 1983; Grime *et al.* 1986; Gaude and Keddy 1988). Slower growing species may then be denied access to space (Schulze *et al.* 1986), nutrients, moisture (Grime *et al.* 1986; Aerts *et al.* 1991) and light (Givnish 1988; King 1991a and 1991b). Slower growing species, however, may be better adapted to surviving periods of restricted resource supply (Grime and Hunt 1975). Thus, when light, water or nutrient resources are abundant, seedlings of those species with innately high growth rates may be advantaged, but low growth rates may be an adaptive advantage to resource limitation. However, differences in (a) seed size or timing of the onset of growth (Benjamin and Hardwick 1986), (b) response to variation in environment (Grime and Hunt 1975), and (c) allocation of plant carbohydrate into resource harvesting structures (Roush and Radosevich 1985), may overide growth rate as the main determinant of seedling size. Consequently, the ecological significance of plant growth rates and productivity on competitive outcomes between seedlings or juvenile plants is dependent on the specific conditions in which the plant is grown and whether or not a particular growth rate enhances the chance of survival within a plant community (Van Andel and Biere 1989).

High growth rates in variable environments may be attained by foraging for resources. Biomass partitioning to shoot or root tissue, may project roots and leaves into resource abundant patches which may increase resource supply and growth (Grime *et al.* 1986). Thus, morphological plasticity may enhance competitive ability when resource availability is patchy. Alternatively, when resources are chronically in short supply, physiological rather than morphological plasticity may be advantageous (Grime *et al.*

1986). Short-term reversible physiological responses may maximise resource utilization when resources are available during brief periods. Thus, both morphological and physiological responses which enhance resource acquisition, are important means contributing to carbohydrate supply for growth and reproduction.

Plant physiological responses to low or high light may influence both biomass gain and water use. Light-limited carbon assimilation may be ameliorated by physiological adaptations which reduce respiratory costs (Bjorkman 1981). Additionally, under variable sub-canopy light environments (eg. sunflecks), modification of the biochemical processes of photosynthesis may increase rates of carbon assimilation (eg. Pearcy 1988). Rainforest canopy species world-wide are characterised by low photosynthetic saturating irradiance, low respiration rates and low light compensation points (Bazzaz and Pickett 1980; Oberbauer and Strain 1985; Givnish 1988; Thompson *et al.* 1988 and 1992), attributes which contribute to positive carbon balance under low and variable light conditions.

The radiant energy associated with high light may increase leaf temperatures, which, in turn, may increase the gradient of water vapour pressure between leaf mesophyll and the atmosphere. Such an increase in evaporative demand may be deleterious to the maintenance of leaf water content when soil moisture is low. Drought avoidance in tree species may be achieved by: (1) maintenence of high rates of water supply through extensive root systems, (2) increased water use efficiency, and (3) reduction of water loss by restriction of transpiration or shedding of leaves (Doley 1986; Osmond *et al.* 1987). However, restriction of water loss by stomatal closure may entail photosynthetic costs due to the limitation of carbon dioxide for photosynthesis (Cowan 1982). Drought susceptible tree species, on the other hand, may be characterised by (a) high stomatal conductances at low water potentials, (b) high cuticular conductances, and, (c) low root area to leaf area ratios (Doley 1986). Other mechanisms by which species avoid excessive leaf evaporative demand include reducing intercepted radiation through

leaf orientation (eg. Anderson 1981) and changes in leaf albedo (eg. Ehleringer and Werk 1986).

Resource availability varies along natural light and water gradients in mountainous terrain due to the interaction between irradiance and topography. Therefore, differences between rainforest and eucalypt species in growth, biomass partitioning and water use characteristics may be important in determining differences between the vegetation types in establishment, growth and survival on natural light and water gradients.

Outline of thesis, aims and hypotheses.

The focus of this thesis is plant responses to variation in light and water resources in rainforest and eucalypt forest species from southeastern New South Wales at the scale of seedlings and adult trees. It was considered that examining processes at the whole plant scale was the appropriate level at which plant responses may be placed in the context of vegetation distribution patterns. Differences in growth and water use by rainforest and eucalypt species may be fundamental to establishment and growth on natural light and water gradients. Understanding plant responses to variation in microenvironment is fundamental to establishing a mechanistic basis of forest vegetation dynamics in eastern Australia. A quantitative understanding of the processes controlling forest distribution is necessary to ensure adequate conservation of Australia's biological resources, and to formulate forest management practices particularly during periods of climate change. In addition, experimental investigation of plant responses to microenvironment will contribute towards understanding the role of plant physiology in the ecology of plant communities. Experimental studies in the present work were conducted to investigate three topics:

Topic 1: Seedling growth, biomass partitioning and water use in response to variation in light and water resources.

Two glasshouse experiments were conducted with the aim of investigating seedling responses to variation in light and water availability. The results of this investigation are presented in Chapter 2. Plant growth, biomass partitioning, transpiration, water uptake and water relations were studied in response to variation in irradiance, soil moisture and nutrient treatments in pot grown rainforest, ecotone and eucalypt forest species from southeastern New South Wales. The results are discussed in terms of the possible implications of seedling growth, biomass partitioning and water use on rainforest and eucalypt species establishment in the field. The hypothesis examined in the first topic was:

> Hypothesis 1: Eucalypts will display physiological characteristics which enhance growth under high irradiance and low soil moisture, whereas rainforest species will display characteristics which are beneficial to growth at low irradiance and high soil moisture. Therefore, differences in plant growth, biomass partitioning and water use in seedlings will be expected between rainforest and eucalypt forest species.

Topic 2: Quantification of canopy structure in rainforest and eucalypt forest.

Forest water use may partly depend on canopy structure. It is apparent that considerable variation in structure occurs between rainforest and eucalypt forest canopies. Thus, it was considered important to quantify differences in leaf area and leaf inclination in each forest type. However, the height of the trees and steep terrain at the field site precluded direct canopy access. Consequently, a photographic technique was

used to compare canopy structural characteristics between vegetation types. The second hypothesis examined in this thesis was:

> Hypothesis 2: Rainforest canopies will have greater leaf area indices than eucalypt forest canopies, whereas leaf inclination angles in the canopies of eucalypt forest will be greater than rainforest. Therefore, differences in leaf area index and average leaf inclination angle will be expected between rainforest and eucalypt forest. Additionally, differences in canopy structure will be related to differences in water use characteristics by each forest type.

This hypothesis was considered in Chapter 3 where differences in canopy structure and vegetation features between rainforest and eucalypt forest are quantified for four experimental plots in a forested catchment in southeastern New South Wales. The trees used on each plot were also used in Chapter 5.

Topic 3: Tree water use, canopy transpiration and conductance to water vapour.

Rainforest and eucalypt forest distribution patterns throughout eastern Australia are associated with aspect. Differences in slope angle and aspect may result in differences in soil moisture content between exposed and sheltered aspects. Additionally, perceived differences in canopy characteristics between rainforest and eucalypt forest were expected to influence canopy transpiration rates. Consequently, it was considered important to investigate transpiration and conductance to water vapour in canopy rainforest and eucalypt forest trees on contrasting aspects. Again, the steeply sloping terrain precluded direct canopy measurements. Thus, sap flow measured at the stem base using the heat pulse velocity technique, was used to estimate transpiration from the canopy. The aim of this experiment was to investigate spatial and temporal variation in

water use characteristics in rainforest and eucalypt trees on opposing aspects within a single catchment. A validation of sap flow measured by the heat pulse velocity technique in saplings of rainforest and eucalypt species is presented in Chapter 4. The third hypothesis investigated in this thesis is:

> Hypothesis 3: Eucalypt species will display conservative water use characteristics consistent with their occurrence on exposed aspects and ridge tops. Rainforest species, however, will display high rates of water use consistent with their position on sheltered aspects and gully bottoms. Thus, differences in canopy transpiration and conductance to water vapour will be expected between rainforest and eucalypt forest trees at different positions on slopes above the gully bottom and on different aspects.

This hypothesis was considered in Chapter 5.

In Chapter 6 results from preceeding chapters are integrated into a conceptual model depicting the processes controlling rainforest and eucalypt forest distribution and also the role of fire in maintaining these forest patterns.

Species selected for laboratory and field studies were representative of rainforest and eucalypt forest canopy trees from southeastern New South Wales. Species used in glasshouse studies were typical of forests at altitudes between 400 and 600 m. Later selection of species for field studies was constrained by site location at a lower altitude (<200 m). There was no difference in dominant rainforest species between low and high altitude sites, but there were differences in eucalypt species between sites. Between 400 and 600 m altitude, *Eucalyptus sieberi* and *Eucalyptus fastigata* were considered representative of the eucalypt forest, whereas *Eucalyptus maculata* was typical of the lower altitude forest. While morphological and physiological differences

occur between these eucalypt species (eg. Bachelard 1986a and 1986b), such differences were less than those between eucalypts and rainforest species.

Table 1.1.
Summary of the variation in microclimate with aspect, and associated variation in vegetation characteristics of forest and understorey species. Data derived from published reports. Symbols are: '+', exposed > shaded slope; '-', shaded > exposed slope; '=', shaded = exposed slope; 'o', no data presented.

Source references are:

a. Washington, USA, 48°N; Turesson (1914)
b. Selkirk Mountains, Canada, 52°N; Shaw (1916)
c. Idaho, USA,47°N; Gail (1921)
d. Colorado, USA, 39°N; Bates (1923)
e. Arizona, USA, 32°N; Shreve (1924)
f. Virginia, USA, 38°N; Platt (1951)
g. New Jersey, USA, 41°N; Cantlon (1953)
h. United Kingdom, 52°N; Ludwig *et al.* (1957)
i. North Carolina, USA, 35°N; Mowbray and Oosting (1968)
j. Sweden, 66°N; Lundqvist (1968)
k. West Virginia, USA, 39°N; Lee and Sypolt (1974)
l. North Carolina, USA, 35°N; Day and Monk (1974)
m. Lathkilldale, UK, 52°N; Rorison and Sutton (1975)
n. Australia, 35°S; Ashton (1976)
o. Kentucky, USA, 37°N; Hutchins *et al.* (1976)
p New Zealand, 43°S; Radcliffe (1982)
q. Virginia, USA, 38°N; Meiners *et al.* (1984)
r. West Virginia, USA, 39°N; Tajchman and Lacey (1986)
s. Australia, 35°S; Tajchman and Lacey (1986)
t. West Virginia, USA, 38°N; Feldhake and Boyer (1990)
u. West Virginia, USA, 38°N; Boyer and Feldhake (1991)
v. Minnesota, USA, 45°N; Hairston and Grigal (1991)

	Source																						% score		
	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r	s	t	u	v	+	-	=
Microclimate																									
Soil temperature	+	o	+	+	+	+	+	+	+	+	+	o	+	o	+	o	o	o	o	o	o	o	57	0	0
Air temperature	o	o	+	o	o	+	+	o	+	+	+	o	+	+	+	o	o	o	o	o	o	o	43	0	0
SMC[a]	-	o	-	-	o	-	o	o	-	o	-	o	-	o	-	o	-	o	o	=	o	-	0	48	5
Humidity	-	o	-	o	o	-	-	o	o	-	-	o	o	o	-	o	o	o	o	-	o	o	0	48	0
Wind speed	o	o	+	o	o	o	=	o	=	=	o	o	o	o	o	o	o	o	o	+	o	o	10	0	14
Irradiance	o	o	o	o	o	o	o	o	o	+	+	o	+	+	+	o	o	o	o	+	+	o	33	0	0
Evaporation	o	o	+	+	o	o	o	o	o	o	o	o	o	o	+	o	o	+	+	+	o	o	24	0	0
Vegetation																									
Diversity[b]	-	-	o	o	o	-	-	o	-	o	o	o	o	o	-	o	o	o	o	o	o	o	0	29	0
Biomass[c]	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	-[e]	o	-	-	+[e]	o	o	5	14	0
Basal area	o	o	o	o	o	o	-	o	o	o	-	-	o	-	-	o	o	o	o	o	o	=	0	24	5
Frequency[d]	o	o	o	o	o	o	-	o	o	o	o	-	o	+	-	o	o	o	o	o	o	o	5	14	0

a Soil moisture content.
b Species diversity.
c Above ground biomass.
d Stem frequency.
e Pasture species.

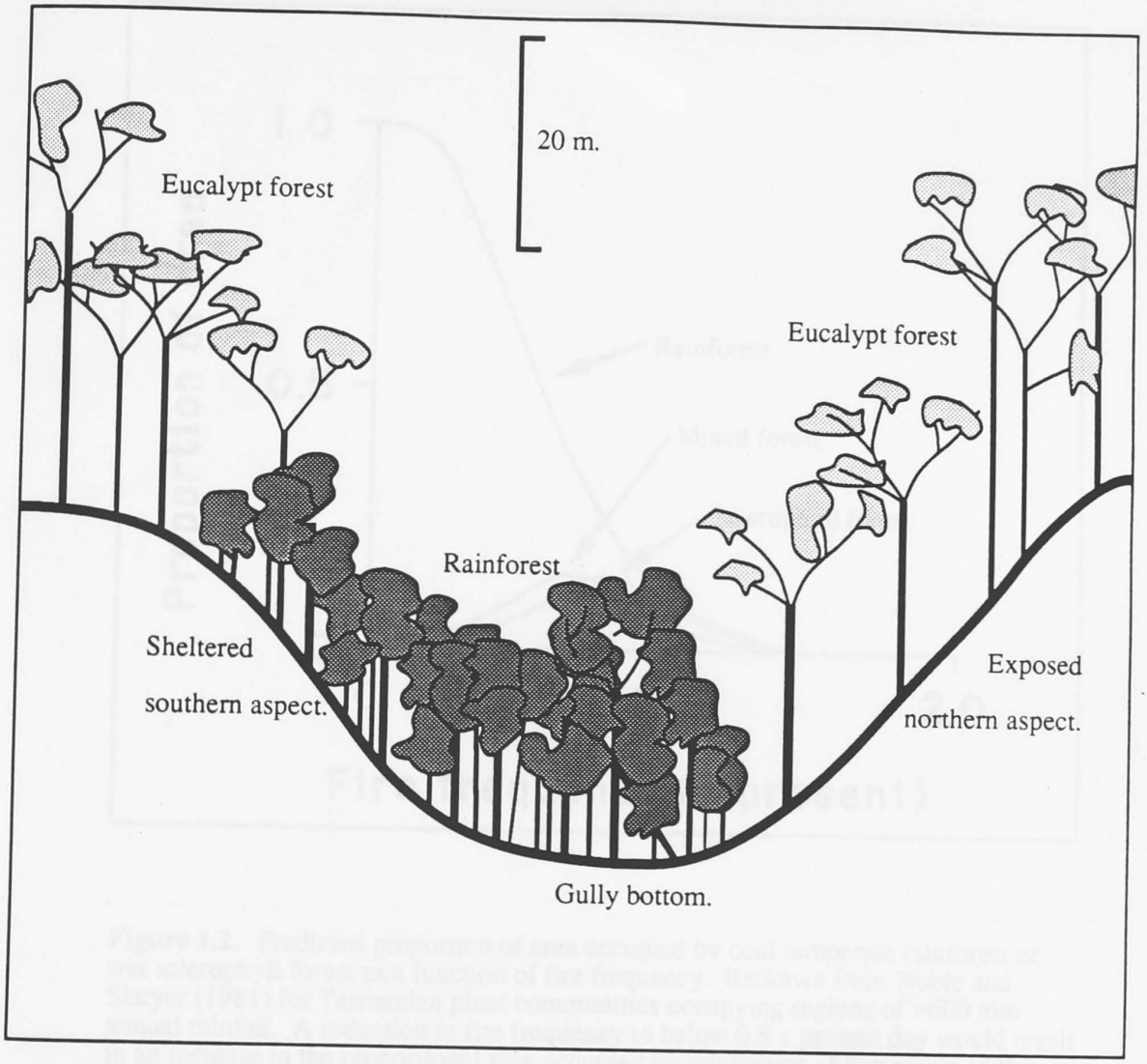


Figure 1.1. Idealised distribution of rainforest and eucalypt forest in relation to aspect in temperate latitudes of eastern Australia.

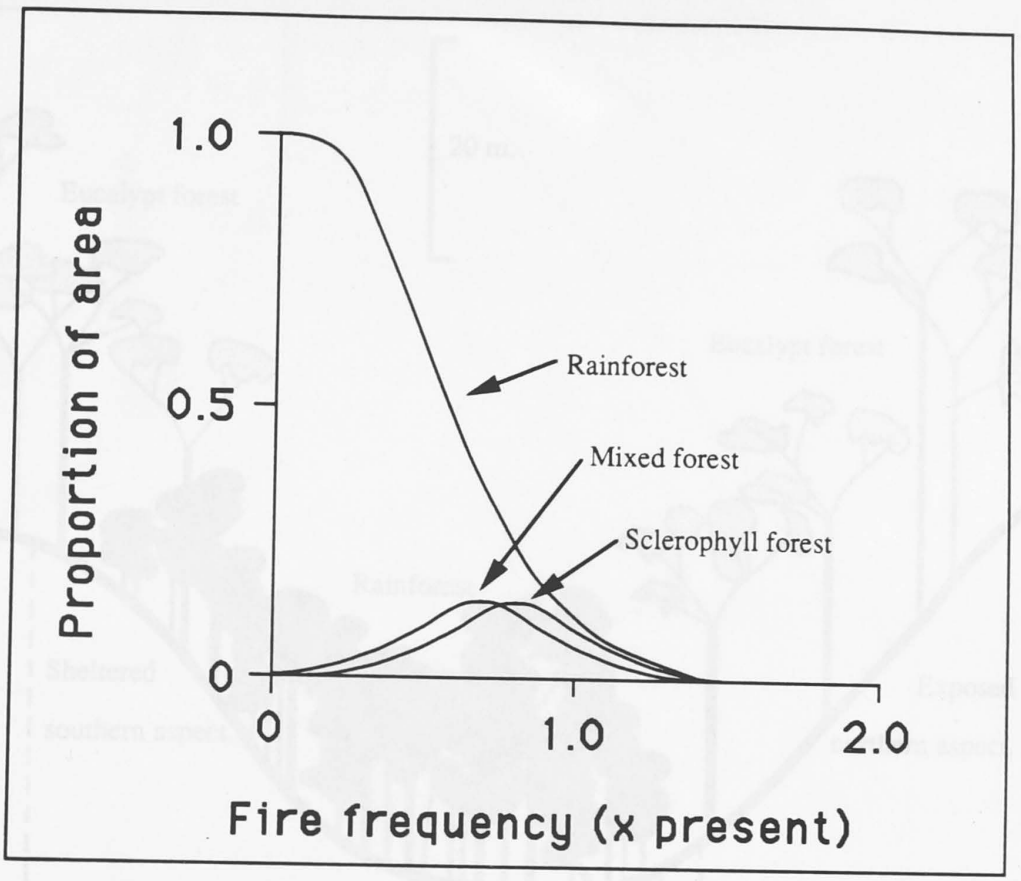


Figure 1.2. Predicted proportion of area occupied by cool temperate rainforest or wet sclerophyll forest as a function of fire frequency. Redrawn from Noble and Slatyer (1981) for Tasmanian plant communities occupying regions of >600 mm annual rainfall. A reduction in fire frequency to below 0.8 x present day would result in an increase in the proportional area occupied by rainforests. Elimination of fire would produce the eventual removal of sclerophyll communities.

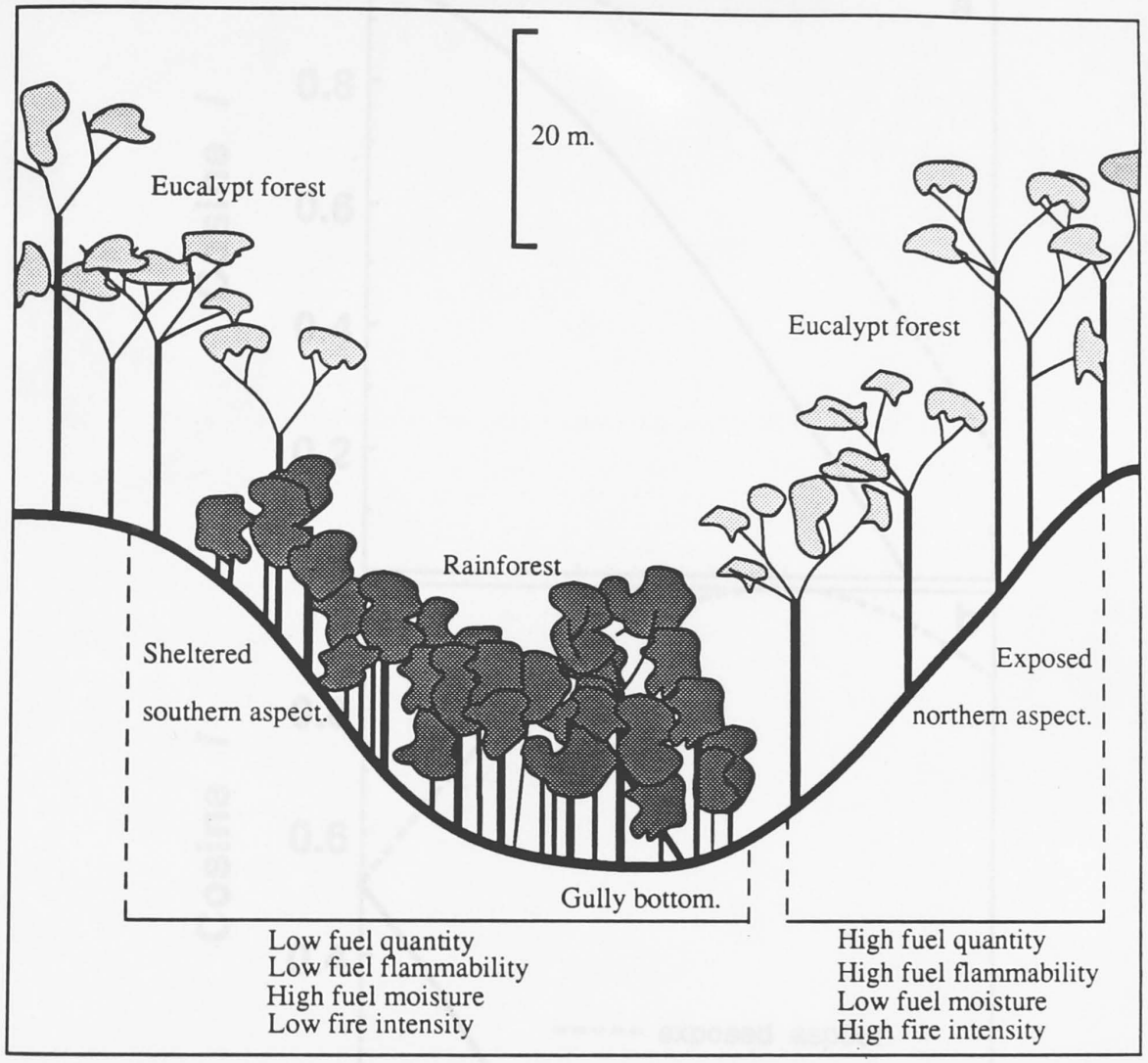


Figure 1.3. Schematic representation of the components controlling fire intensity in relation to aspect, slope angle and vegetation distribution. Maximum fire intensity would be expected on exposed aspects where slope angle interacts with relatively high fuel loads. Minimum fire intensities would be expected in rainforest where fuel load is relatively low. Fire direction is dependent on prevailing wind at the time of fire.

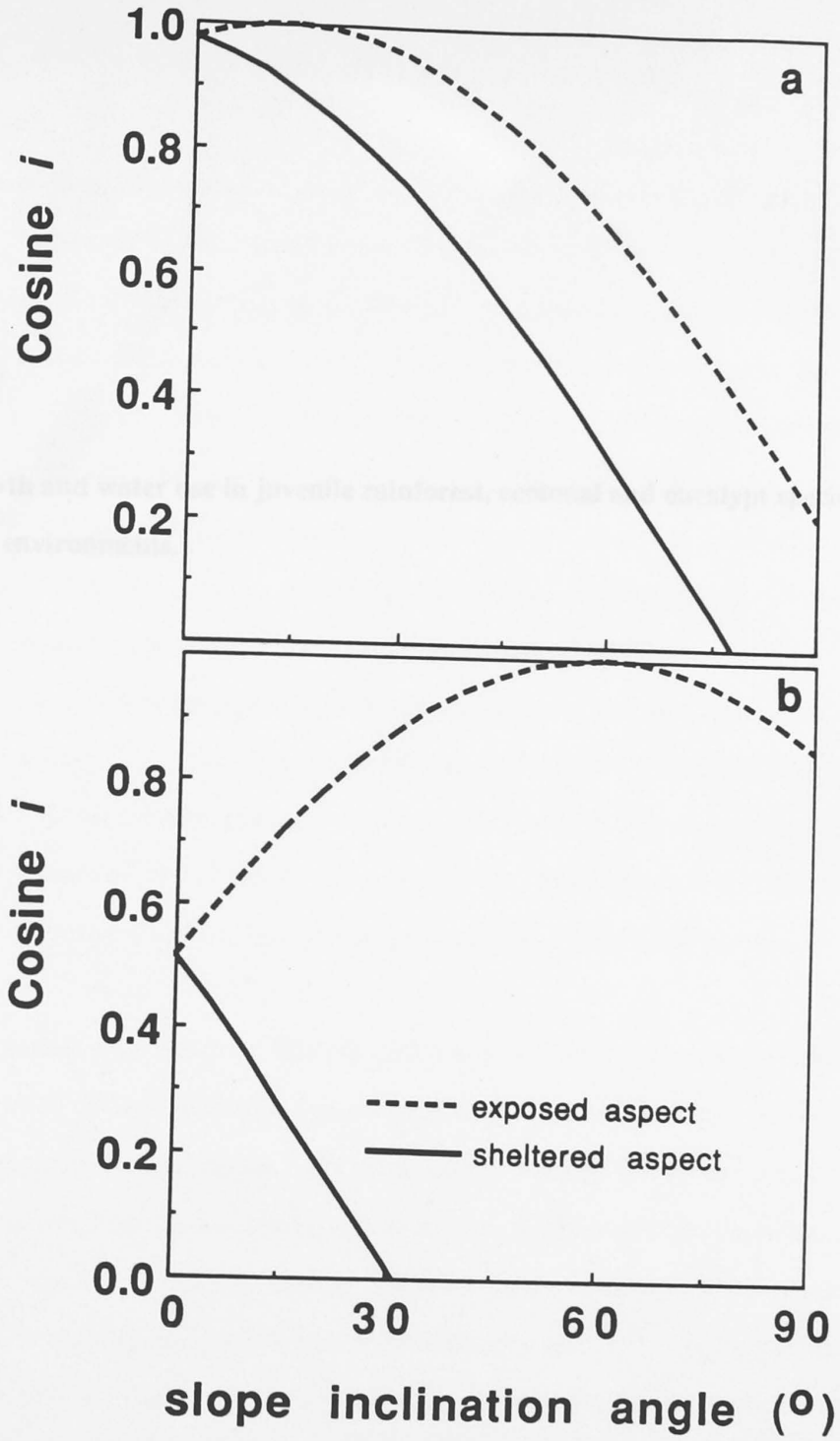


Figure 1.4. The relationship between ground surface slope angle and cos *i* for exposed (north facing) and sheltered (south facing) aspects on (a) the summer and (b) the winter solstice at solar noon for latitude 35° 30'.

Chapter 2.

Plant growth and water use in juvenile rainforest, ecotonal and eucalypt species in controlled environments.

Abstract

Differences in plant growth and water use by rainforest, ecotonal and eucalypt forest species from southeastern New South Wales, were studied in two glasshouse experiments. In the first experiment, growth of these species was studied in relation to variation in light, water and nutrients. The species studied were *Eucalyptus sieberi* and *Eucalyptus fastigata,* which inhabit relatively high light environments of exposed aspects, upper sheltered aspects and ridge tops in the gully systems of south coastal New South Wales, *Callicoma serratifolia, Pittosporum undulatum* and *Elaeocarpus reticulatus,* which are pioneer species of the ecotone around rainforest patches, and *Backhousia myrtifolia* and *Ceratopetalum apetalum,* which are rainforest canopy species. Biomass was maximal under relatively high levels of soil moisture, nutrients and light. Under high irradiance (1230-1670 μmol PAR m^{-2} s^{-1}) mean biomass was ranked as follows: eucalypt species > ecotonal species and *B. myrtifolia* > *C. apetalum.* At low irradiance (200-530 μmol PAR m^{-2} s^{-1}) the reverse trend was observed, such that rainforest canopy and ecotone species produced the greater plant biomass.

Biomass partitioning indicated relative differences in plant responses to treatments. The proportion of plant mass partitioned to leaf mass (leaf weight ratio) did not change between experimental treatments. The magnitude of the response of leaf area ratio and specific leaf weight to light treatment, however, was ranked as follows: eucalypt species > ecotone species > rainforest canopy species. The species which occur naturally outside the rainforest canopy had greater leaf area per unit plant mass under the 200-530 μmol m^{-2} s^{-1} light treatment, which may contribute to biomass gain at low irradiances.

In the second experiment, two eucalypt species (*Eucalyptus sieberi* and *Eucalyptus fastigata*) and four rainforest species (*Acmena smithii, Baloghia inophylla, Doryphora sassafras* and *Ceratopetalum apetalum*) were grown in glasshouse conditions under

three light (4-6%, 21-42% and 65-88% full sunlight) and three soil water (80%, 51% and 26% field capacity) treatments. Plant biomass increased with an increase in irradiance from 4-6% (80-130 μmol m^{-2} s^{-1}) to 21-42% sunlight (440-880 μmol m^{-2} s^{-1}) in all species. However, further increase in irradiance to 65-88% sunlight (1370-1850 μmol m^{-2} s^{-1}) did not necessarily increase biomass. Under both medium and high light treatments, eucalypt species produced more biomass than rainforest species, whereas rainforest species produced more biomass than eucalypts at 4-6% sunlight. Plant biomass increased with an increase in soil moisture in all species except *D. sassafras* and *C. apetalum*. Biomass partitioning to roots increased relative to leaves and stems with increasing irradiance, thereby increasing root mass per unit leaf area and root:shoot ratio. At the end of the experiment, shoot transpiration rates were not significantly different between species, light or water treatments, with a mean transpiration rate (per unit leaf area) for all species and treatments of 1.75 mmol m^{-2} s^{-1}. Similar transpiration rates between species and treatments, may be due to the variation in biomass partitioning between water uptake and water loss structures in response to light and water treatments. Rates of water uptake per unit root dry weight were higher in eucalypts at low irradiance. In contrast, rates of water uptake did not change in rainforest species under different light treatments. No differences in plant water relations were observed between species of each vegetation type.

Introduction

Much of the terrain along the southern coast of New South Wales, is mountainous and rugged, resulting in a high degree of spatial variation in light, water and nutrients. The environment on exposed aspects and ridge tops is characterised by relatively high irradiance and low soil moisture (Yates 1989, see also Chapter 5). Conversely, the environment of the gully bottom and sheltered aspects is moister, with lower irradiance. Distribution of rainforest and eucalypt forest is associated with variation in

microenvironment. Rainforest is located along the gully bottom and on sheltered aspects, whereas, eucalypt species occur upslope of rainforest, on exposed aspects and ridge tops (Yates 1989, see also Chapter 3). This differential distribution of rainforest and eucalypt forest with aspect may be due to factors controlling seedling and sapling growth and survival along natural light and water gradients.

Results from two glasshouse experiments are reported in this chapter. In the first experiment, plant growth and biomass partitioning in response to variation in light, water and nutrient treatments were studied in seven species from rainforest, ecotonal and eucalypt vegetation. In the second experiment, growth, biomass partitioning, transpiration, water uptake rates and water relations were studied in six species from rainforest and eucalypt forest under different light and soil moisture treatments. The first hypothesis (Chapter 1) proposed that eucalypt species would possesscharacterisitics which may enhance plant growth under high irradiance and low soil moisture, whereas rainforest species would display characteristics which may enhance growth under low irradiance and high soil moisture. Relative differences in plant growth, biomass partitioning and water use between species under experimental treatments may indicate plant responses which increase growth and promote survival under different light, soil moisture and nutrient conditions in the field.

Methods

Selection of species.

Species were chosen to represent canopy and sub-canopy trees of rainforest, ecotonal and eucalypt vegetation in southeastern coastal New South Wales. Seven species were used in the first experiment. At altitudes between 500 and 1000 m *Eucalyptus sieberi* attains heights of 25-35 m (Boland *et al.* 1984). This species dominates ridges and

exposed (north facing) aspects to just above the gully bottom, where it typically forms an abrupt boundary with rainforest (Austin 1978). On sheltered (south facing) aspects the dominant eucalypt canopy species is typically *Eucalyptus fastigata*, which reaches heights of 30-45 m (Boland *et al.* 1984), and overtops rainforest species where they co-occur. *Pittosporum undulatum* is a small tree up to 12m high, found within the rainforest ecotone and upslope on sheltered aspects beneath a *E. fastigata* overstorey. *Callicoma serratifolia* is a rapidly growing tree, up to 25 m high, abundant in the ecotone, disturbed patches of rainforest and along water courses (Floyd 1989) where it may form a sharp boundary with eucalypt forest. *Elaeocarpus reticulatus* is a shrub or small tree up to 10 m and is associated with the ecotone on sheltered aspects. *Backhousia myrtifolia* is a rainforest canopy species of littoral and dry rainforest patches, often on shallow rocky soils, where it forms pure stands (Helman 1983). *Ceratopetalum apetalum* is a common rainforest canopy species, up to 30 m high (Floyd 1989).

For the second experiment, six tree species were chosen as representative of rainforest and eucalypt vegetation. Both *E. fastigata* and *E. sieberi* were again chosen as representative of eucalypt forest. In addition to *Ceratopetalum apetalum* and *Doryphora sassafras, Baloghia inophylla* and *Acmena smithii* were also selected as representative of rainforest. At altitudes between sea-level and 400 m the rainforest canopy in southeastern New South Wales, is dominated by *C. apetalum, A. smithii* and *D. sassafras* (Helman 1983; Floyd 1989; Ashton and Frankenberg 1976; Melick 1990a and 1990b). These three species reach 35 m in height and regenerate beneath the rainforest canopy. Seedlings of *C. apetalum* and *D. sassafras* are occasionally found outside rainforest in locations of high soil moisture but generally not on exposed aspects which receive high irradiance. *Acmena smithii* is sometimes found outside the rainforest as seedlings or saplings on sheltered aspects and occasionally on exposed aspects. *Baloghia inophylla* is a sub-canopy rainforest tree up to 20 m height, which regenerates beneath the canopy (Floyd 1989), and is rarely found outside the rainforest.

Plant culture.

In January 1990, cuttings of *C. apetalum, E. reticulatus, B. myrtifolia, P. undulatum, C. serratifolia, D. sassafras, A. smithii* and *B. inophylla* were collected from saplings and juvenile plants in a single rainforest patch (35° 34' S, 150° 02' E). This rainforest is a representative of Simple Notophyll Vine Forest, using Webb's (1968) physiognomic classification, and of the *Ceratopetalum/Schizomeria-Acmena-Doryphora* Suballiance using Floyd's (1990a and 1990b) floristic classification system for New South Wales rainforest. All leaves were sprayed with water to reduce transpiration before removal of cuttings, which were immediately placed in a pre-wetted, black plastic bag for transport. Each cutting (<8 cm length) consisted of at least two leaf nodes and new growth on green stems. The leaves at the lowest node were cut off at the base of the petiole and 75% of the leaf lamina was cut from the leaves at the top node. The basal end of the cutting was dipped, for 10 seconds, in 8000 ppm indole-3-butyric acid (Sigma Chemical Company). Cuttings were potted in a 1:1:1 peat:sand:perlite mix and positioned under a misting spray for 4 weeks. By this time root formation was observed and plants were hardened off in a glasshouse for a further 4 weeks, then repotted in 15 cm pots (Volume = 1.8 L). Plants were watered daily and fertilised with 130 ml Aquasol fertiliser (1 g L^{-1}) in weeks 11 and 13 after planting. At the end of week 17 plants were placed in treatments. By then, the original stem had developed woody tissue, the original leaves had abscised and the root system appeared similar to that of juveniles of a similar size (up to 10 cm height) in the field. Because cuttings were taken from shoot tips, near the base of saplings and juveniles, they were assumed to respond to treatments similar to plants grown from seed.

Eucalypt species were grown from seed collected by the Tree Seed Centre (CSIRO, Division of Forestry). Seeds of *E. fastigata* were collected at 35° 49' S, 149° 30' E and *E. sieberi* at 35° 32' S, 150° 03' E. In January 1990, eucalypt seed was germinated on

moist filter paper at 27°C and then transplanted to 5 cm pots for four weeks, before being repotted into 15 cm pots and grown under the same water and nutrient regime as the rainforest plants.

Experimental design.

(a) Experiment 1: Growth and biomass partitioning in rainforest, eucalypt and ecotonal species.

In the 19th week, five plants of *C. apetalum, E. reticulatus, B. myrtifolia, P. undulatum, C. serratifolia, E. fastigata* and *E. sieberi* were harvested and the length, breadth and area of each leaf was measured. Linear regression was used to establish the relationship between leaf length x breadth and leaf area for each species. These regressions were used to estimate initial leaf area of each plant used in the experiment.

The experimental design consisted of four blocks each containing one plant of each species in each combination of two light treatments, two water treatments and two nutrient treatments. Plants were matched for size and then allocated randomly to blocks in the glasshouse. The two light treatments were "high light"; where plants were exposed to direct sunlight inside the glasshouse, and "low light"; with plants inside frames covered by two layers of nylon shade cloth. These light treatments resulted in plants receiving irradiance in the photosynthetically active wavelengths (PAR) at 65%-88% and 11%-28% sunlight throughout the experiment, which corresponded to light levels beneath a eucalypt canopy on exposed and sheltered aspects, respectively. The two water treatments were achieved by administering either 130 ml water ("high water") or 35 ml water ("low water") every 3 days; the high water treatment corresponding to soil water content at field capacity. Nutrient treatments were applied by adding 130 ml Aquasol fertiliser (1 g L^{-1}) to each pot. The "high nutrient" treatment received fertiliser in the 17th, 21st, 25th, 29th, 33rd and 37th week. The "low

nutrient" treatment also received 130 ml of Aquasol fertiliser, but in the 25th and 37th week only.

Plants were grown under treatments until the 41st week, then plants were harvested and divided into root, stem and leaf components. Dry weights of plant parts and leaf area were measured. Several indices of plant response to treatments were calculated: leaf weight ratio (LWR: $g\ g^{-1}$), an index of relative biomass allocation to photosynthetic tissues, leaf area ratio (LAR: $cm^2\ g^{-1}$), the potential photosynthetic area per unit plant biomass, and specific leaf weight (SLW: $g\ cm^{-2}$), the proportion of leaf biomass per unit leaf area. Treatment and interaction effects were tested by analysis of variance, with initial leaf area as covariate, and by multiple linear regression, using Genstat-5 (Lane *et al.* 1987; Digby *et al.* 1989). Total plant dry weight, leaf area and leaf dry weight data were log transformed which removed heteroscedasticity.

(b) Experiment 2: Growth and water use by rainforest and eucalypt species.

In the 17th week after planting, 27 plants of *E. fastigata, E. sieberi, A. smithii, B. inophylla, D. sassafras* and *C. apetalum* were matched for size and allocated to each combination of three light and three water treatments arranged randomly within three replicate blocks. Water treatments were imposed by adding 110 ml, 70 ml and 35 ml of water to the pot every three days, thereby supplying 80%, 51% and 26% field capacity of the soil. The light treatments were imposed using layers of nylon shade cloth. The treatments were, uncovered plants (65-88% sunlight), one layer of shade cloth (21-42% sunlight) and two layers of shade cloth (4-6% sunlight). Light conditions corresponded to those beneath an exposed and sheltered aspect eucalypt canopy and a rainforest canopy, respectively. Air conditioning maintained daytime temperatures between 22°C and 32°C. All plants were fertilised again in the 24th and 27th week by adding 130 ml Aquasol fertiliser ($1\ g\ L^{-1}$) to each pot. Plants were harvested after 34 weeks growth under treatments.

Shoot evaporation rates were measured at the end of the experimental period (34th week). Pots were watered to field capacity, weighed 24 hours later and then reweighed each day to determine water loss. Soil evaporation was estimated from three pots without seedlings in each light treatment, and subtracted from daily water loss to calculate shoot water loss. Mean daytime shoot transpiration rates (E) were calculated as,

$$E = \frac{W}{L\,T} \qquad (2.1)$$

where W is shoot water loss (mole), L is shoot leaf area (m^2) and T was the diurnal photoperiod (49,500 seconds), assuming negligible shoot transpiration at night. Plant water status was measured when shoot transpiration rates had decreased to zero. Plants were placed in a dark room overnight. The pre-dawn water potential (Ψ) of the apical shoot of each plant was determined by the pressure-equilibrium method (Turner 1981, 1988). Immediately afterwards a cork borer was used to punch thirteen 0.18 cm^2 leaf discs from the youngest fully formed leaf. Four of these discs were placed in a micro-Eppendorf tube and plunged into liquid nitrogen before being stored at -20^{o}C for 2 to 10 days. These leaf discs were used to determine osmotic potentials (π) of leaf tissue using a dew point microvoltmeter (Model HR-33T, Wescor Inc., Utah, USA). Leaf water content (g H_2O g^{-1} leaf dry weight) and succulence (g H_20 m^{-2} leaf area) were measured from the remaining leaf discs by determining fresh weight on an electronic balance, then drying at 80^{o}C for five days and reweighing. The remainder of each plant was divided into root, shoot and leaf portions. Leaf area was measured with an electronic planimeter (Paton Scientific Pty. Ltd., Australia). All plant portions were then dried in an oven at 80^{o}C for five days and weighed. Dry weights and leaf area measurements were used to calculate leaf weight ratio (LWR: g leaf g^{-1} plant), leaf area ratio (LAR: cm^2 leaf area g^{-1} plant), specific leaf weight (SLW: g leaf cm^{-2} leaf area),

root:shoot (g root g^{-1} shoot), root mass:leaf area (g root cm^{-2} leaf area) and stem height:stem weight ratios (cm height g^{-1} weight). Analysis of variance was used to determine significant treatment and interaction effects using Genstat-5 (Lane *et al.* 1987; Digby *et al.* 1989). Dry weights and leaf area data were logarithmically transformed, which removed heteroscedasticity.

Results

Experiment 1: Growth and biomass partitioning in rainforest, eucalypt and ecotonal species.

(a) Initial leaf area

Regression of leaf area as a function of leaf width x breadth (Table 2.1) produced coefficients of determination (r^2) greater than 0.97. This procedure provided accurate estimates of initial leaf area for each plant. The estimated initial leaf area was used as a covariate in the analysis of variance, to determine and remove the influence of variation in initial plant size from treatment effects. The covariance efficiency factor is the ratio of the mean square before and after adjusting for the covariate (Digby *et al.* 1989). A covariance efficiency greater than unity indicates a reduction in unexplained variance in the analysis, whereas a value approaching zero suggests that treatment effects were eliminated by the covariate. For the light treatment in the analysis of variance, the covariate efficiency factors were 0.74, 0.75 and 0.82 for mean dry weight, leaf area and leaf dry weight, respectively. This indicated partial correlation between initial leaf area and the light treatment, possibly due to the 15 day period between placing plants within light treatments and measuring leaf dimensions of each plant. The 15 day period appears to have been sufficient to allow some measurable plant response to light treatments. For water and nutrient treatments, covariate efficiencies were between 0.88

and 0.98, suggesting little or no correlation between treatments and initial plant size. Covariate efficency factors of the residual, for all interaction terms in the analysis of variance, were 2.1, 1.75 and 1.87 for dry weight, leaf area and leaf dry weight, respectively. The increase in covariance efficency of the residual term indicates a reduction in the unexplained variance after inclusion of the covariate. Thus, differences in plant size at the begining of the experiment were removed by the covariate. The covariate had little or no influence in the analysis of LWR, LAR and SLW, with covariate efficiencies of 1.00, 1.03 and 0.99, respectively.

(b) Plant growth characteristics.

Analysis of variance for total dry weight indicated significant individual treatment effects, significant two-way interactions between treatments, and significant species x treatments effects (Table 2.2). Total dry weight increased at high irradiance in all species ($P<0.01$, Fig. 2.1a), at high nutrient levels in *E. sieberi, E. fastigata* and *P. undulatum* ($P<0.01$, Fig. 2.1c), and at high water treatments in *E. sieberi* and *C. serratifolia* ($P<0.01$), *E. fastigata,* and *P. undulatum* ($P<0.05$, Fig. 2.1b). An increase in irradiance at the high water treatment increased mean total dry weight, averaged over all species, from 0.65 g to 3.88 g ($P<0.01$. Table 2.3). Similarly, the higher nutrient treatment under high irradiance and under high water treatment, increased mean total dry weight, averaged over all species, from 2.81 g to 3.80 g ($P<0.05$) and from 1.34 g to 1.90 g ($P<0.01$), respectively.

Both water and nutrient treatments were significant in the ANOVA of leaf area and leaf dry weight (Table 2.2). Mean leaf area increased significantly ($P<0.01$) from low water (51.7 cm^2) to high water (61.3 cm^2) and from low nutrient treatment (49.7 cm^2) to high nutrient treatment (63.9 cm^2). Additionally, all two-way interactions except light x nutrient, were significant. Increasing irradiance under the high water treatment

increased mean leaf area from 31.0 cm^2 to 121.2 cm^2 ($P<0.01$, Table 2.3). Similarly, increasing water treatment under high nutrient conditions increased mean leaf area from 55.1 cm^2 to 74.1 cm^2 ($P<0.05$).

Interactions between light x species and water x species on leaf area were similar to those on total plant dry weight. Mean leaf area increased greatly ($P<0.01$, Fig. 2.1d) under high irradiance in *E. sieberi, E. fastigata, B. myrtifolia,* and *P. undulatum*, and also in *E. reticulatus, C. serratifolia* and *C. apetalum* ($P<0.05$). Leaf area increased significantly under high water treatment in *C. serratifolia* ($P<0.01$) and *P. undulatum* ($P<0.05$, Fig. 2.1e) and under high nutrients in *E. sieberi, E. fastigata, P. undulatum* ($P<0.01$, Fig. 2.1f), but decreased in *C. serratifolia* ($P<0.05$).

Mean leaf dry weight showed similar trends to total dry weight, and increased significantly ($P<0.01$, Table 2.2) under high water treatment from 0.66 g to 0.80 g, and under high nutrient treatment from 0.65 g to 0.81 g. Additionally, all two-way interactions and species x treatment interactions showed the same trend as was observed for total plant dry weight and leaf area.

(c) Biomass partitioning.

Leaf weight ratio (LWR), leaf area ratio (LAR) and specific leaf weight (SLW) did not vary between different light, water and nutrient treatments (Table 2.2). However, species differences were apparent, as was a significant light x species interaction for LAR and SLW which is discussed below. None of the two-way treatment interactions in the analysis of variance were significant.

The light treatment had no effect on LWR in any species (Fig. 2.2a), suggesting that the proportion of biomass allocated to source and sink regions of the plant remained

constant between species in all treatments. All species responded to low light treatments by increasing leaf area relative to plant biomass, thereby increasing LAR. Only the eucalypts, however, showed a significant response ($P<0.05$, Fig. 2.2b), with the range of difference exceeding that in all other species. Specific leaf weight decreased at low irradiance. Both eucalypt species responded to low light treatments by more than doubling potential photosynthetic area relative to leaf biomass. Similarly, *C. serratifolia* and *P. undulatum*, both ecotonal species, decreased SLW significantly under low light treatment ($P<0.01$ and $P<0.05$, respectively). At low irradiance, SLW was significantly higher in *C. apetalum* than in both eucalypts ($P<0.05$) and, conversely, SLW was significantly lower in *C. apetalum* than *E. sieberi* at high light levels ($P<0.05$), indicating proportionally greater leaf biomass per unit leaf area at the low irradiance in *C. apetalum*.

Multiple regression analysis was used to investigate the relationship between leaf weight and whole plant biomass (Fig. 2.3a) and leaf weight and leaf area (Fig. 2.3b). In each case there was a linear relationship between the logarithm of final leaf weight and the logarithm of final plant dry weight and final leaf area. The best linear regression model to describe the relationship between leaf weight and plant weight consisted of separate but parallel regression lines through high and low light treatments ($r^2=0.980$, $P<0.01$, Fig. 2.3a). This suggested that, amongst all species for a given plant weight, leaf weight was greater at low irradiance, and that the slope of the relationship did not differ between light treatments. This was in agreement with the difference in LWR observed between light treatments (Fig. 2.2a).

The multiple regression model which best described the relationship between leaf weight and leaf area produced different regression slopes at high and low light treatments ($r^2=0.907$, $P<0.01$; Fig. 2.3b). This model indicated that for a given leaf area, a higher irradiance resulted in a greater leaf weight, and that the slope relating leaf area to leaf weight decreased under low light. Inclusion of the "species" term in the

model produced minor increase in the variance explained (r^2=0.941, P<0.01) due to differences in leaf size and did not alter the relationship between leaf area and leaf weight within a light treatment.

Experiment 2: Growth and water use by rainforest and eucalypt species.

(a) Plant growth

There were significant effects associated with individual treatments and their interactions (Table 2.4). Biomass increased in all species in response to an increase in irradiance from 4-6% to 21-42% sunlight (Fig. 2.4a). A further increase in irradiance to 65-88% sunlight, however, did not further increase mean biomass in all species and some (*C. apetalum D. sassafras*) showed a decline. Only in *E. fastigata* did biomass significantly increase from medium to high light treatments (p<0.05). Biomass of both eucalypt species and *A. smithii*, was greater than the other rainforest species at 21-42% and 65-88% sunlight (p<0.01). The rank order of biomass at high and medium light treatments was *E. fastigata* > *E. sieberi* > *A. smithii* > *B. inophylla* > *C. apetalum* > *D. sassafras*. At low irradiance this trend was reversed and *C. apetalum* produced greater biomass than *E. sieberi* (p<0.10). The rank order of biomass at the end of the experimental period under low light treatments was *C. apetalum* > *A. smithii* > *B. inophylla* > *D. sassafras* > *E. sieberi* > *E. fastigata.*

Biomass increased with increasing water treatment in all species except *C. apetalum* (p < 0.05, Table 2.4, Fig. 2.4b) although individual responses varied between species. Biomass increased by 75% in *E. fastigata* and by 57% in *B. inophylla* with an increase in soil moisture from the 35 to 70 ml treatments. Biomass of *E. sieberi* nearly doubled with an increase in water treatment from 70 and 110 ml. *Acmena smithii* maintained the highest biomass in low and medium water treatments, whereas, the increase in mean biomass in *Doryphora sassafras* was less than other species with increasing soil

moisture. Mean biomass in *C. apetalum* decreased with increase in soil moisture by 8% from 35 to 70 ml water treatments.

Root dry weight and leaf dry weight changed in response to increased light and water in the same way as biomass (Fig. 2.4c, 2.4d, 2.4e and 2.4f; Table 2.4), with two exceptions: (a) In *E. sieberi,* mean root dry weight decreased by 13% with an increase in irradiance form medium to high light treatment (Fig. 2.4c), and (b) leaf dry weight of *A. smithii* declined by 17% between medium and high light treatments (Fig. 2.4e). The water x species interaction for leaf dry weight was marginally not significant ($p < 0.1$, Table 2.4), although the observed trend was identical with root dry weight (Fig. 2.4f).

Maximum leaf area was produced at medium irradiance in all species (Fig. 2.4g). This trend was particularly pronounced in *E. fastigata, E. sieberi* and *A. smithii*, which decreased leaf area by 34%, 23% and 26% from medium to high irradiance, respectively. The water x species interaction for leaf area (Fig. 2.4h) was not significant (Table 2.4).

(b) Biomass partitioning

Dry mass partitioned to roots averaged over all species, increased significantly relative to biomass partitioned to leaves and stems in response to increasing irradiance (Table 2.5). However, variation in water treatment did not change stem or leaf biomass fraction.

Variation in root:shoot ratio in response to light treatment, differed between species ($P < 0.05$, Table 2.6) but there were no consistent differences between vegetation types (Fig. 2.5a). Root:shoot ratio increased with increasing irradiance in *E. fastigata, B. inophylla* and *C. apetalum* by 104%, 44% and 72% between low and high light

treatments. Root:shoot ratio, however, decreased in *E. sieberi* by 26%, between medium and high light treatments; a consequence of reduced root mass (Fig. 2.4c). A variable response by root:shoot ratio between species to water treatment, was not significantly different between either species or treatments (Table 2.6, Fig. 2.5b).

Root mass increased relative to leaf area in response to increasing irradiance in all species, and to increasing water treatment in all species except *C. apetalum* and *B. inophylla* (Table 2.6, Fig. 2.5c and 2.5d). *Ceratopetalum apetalum* maintained the highest root mass:leaf area ratio at all light and water treatments. At 4-6% light treatment, biomass partitioned to roots, relative to leaf area, was lower in both eucalypts than in the rainforest species. Partitioning to roots increased in both eucalypt species under higher irradiance.

The light x species term was significant for LAR and SLW, but not LWR (Table 2.6). Leaf area decreased in proportion to plant mass in all species with increasing irradiance (Fig. 2.5e). At 4-6% sunlight LAR of both eucalypt species was greater than rainforest species ($p<0.01$). At higher light treatments, however, LAR was not significantly different between species. SLW increased with increasing irradiance in both eucalypt species ($p<0.05$; Fig. 2.5g), but was not significantly different between light treatments in all other species. The water x species interaction term for LWR, LAR and SLW was not significant (Table 2.6). Consequently, no significant differences were observed in LAR, LWR and SLW in all species, between water treatments (Fig. 2.5f and 2.5h).

Stem height per unit stem weight increased greatly with decreasing irradiance and soil moisture (Fig. 2.6) in some species, but not others. Greater allocation of biomass to stems at low light (Table 2.5) was accompanied by an increase in stem height per unit weight from medium to low light treatment in all species, except *C. apetalum* ($p < 0.01$; Fig. 2.6). In general the greatest response was observed in the eucalypt species with stem height per unit weight increasing by a factor of 4.5 and 4.2 in *E. sieberi* and *E.*

fastigata, respectively. The significant water x species interaction (Table 2.6) was due solely to an increase in stem height per unit weight in *E. sieberi*, by a factor of 2.3, in response to a decrease in soil moisture from 70 to 35 ml water treatments.

(c) Shoot water use.

Shoot transpiration rates were measured at the end of the experimental period, one day after watering all pots to field capacity. On this day (3rd October 1990) air temperature was maintained at around 27°C and water vapour pressure deficit ranged between 260 and 485 Pa throughout the day. There were no significant differences in shoot evaporation rates between either treatments or species (Fig. 2.7a and Table 7).

Rates of water uptake per unit root mass in plants watered to field capacity (Fig. 2.7c), were significantly greater at low irradiance ($p < 0.001$) in *E. sieberi* and *E. fastigata* (58.1 and 66.2 μmol H_20 g^{-1} root dry weight s^{-1}, respectively) than in *D. sassafras* (36.3 μmol g^{-1} s^{-1}), and *A. smithii, B. inophylla* and *C. apetalum* (21.6, 19.6 and 20.1 μmol g^{-1} s^{-1}). Water uptake rates decreased significantly in both eucalypt species ($P < 0.05$), with an increase in irradiance to 21 - 42% sunlight (Fig. 2.7c) and decreased, but not significantly, in rainforest species. Water uptake rates were not significantly different between species at either medium or high light treatments. Additionally, there were no significant water or water x species interaction effects (Table 2.7, Fig. 2.7d).

(d) Shoot water relations

After watering plants to field capacity, pots were allowed to dry until shoot evaporation rates had declined to zero. Then leaf water and osmotic potentials were measured. Table 2.8 shows significant differences in mean water and osmotic potentials at the species level ($P < 0.05$), derived from an analysis of variance. There were species

differences in plant water relations, but no consistent differences between rainforest and eucalypt species. Mean water potential was lowest in *E. sieberi* (-1.88 MPa) and highest in *B. inophylla* (-0.43 MPa). Mean osmotic potential was lowest in *C. apetalum* (-2.51 MPa) and highest in *E. fastigata* (-1.83 MPa). Higher order interaction terms were also significant ($P<0.05$), but no consistant differences between rainforest and eucalypts species were observed.

Mean tissue turgor pressure was estimated for each species by the difference between mean Ψ and mean π (Table 2.8). Cell turgor remained relatively high in both *B. inophylla* and *C. apetalum*, at 1.80 and 1.88 MPa, respectively, whereas lowest mean turgor pressures were found in *E. sieberi* and *D. sassafras* (0.37 and 0.57 MPa respectively).

Differences between leaf water content per unit leaf area (succulence) were apparent on the basis of vegetation type (Table 2.8). Rainforest species generally maintained higher water contents per unit leaf area than eucalypt species. There appeared to be no association, however, between succulence or leaf relative water content, and mean leaf cell turgor, water or osmotic potentials.

Discussion

Results from both experiments were complimentary and are discussed together in terms of the various growth and water use parameters. A summary of relative plant responses by rainforest and eucalypt forest species from both experiments, to variation in light, water and nutrient treatments is given in Table 2.9.

Plant growth.

In the first experiment, estimated initial leaf area was effective as a covariate at removing effects due to different initial plant sizes on final leaf area, leaf dry weight and total biomass (Fig. 2.1). However, covariance between initial plant size and the light treatment, indicated that plants had begun to respond to light treatments within 15 days. Nobel (1980) showed that illumination level during leaf development was important in determining leaf morphology. King (1990b), using a game-theory based model to predict patterns of tree height growth in forests, suggested that competition for light was the primary determinant of allometric relationships between tree height growth and crown size. The results from the present work indicate a rapid response by these tree species to light, particularly in eucalypts.

Whole plant biomass at the end of the first experiment, adjusted for the covariate (Fig. 2.1), was a measure of growth rate. All species produced greater biomass and hence, had higher growth rates under high irradiance (65-88% vs. 11-28% sunlight). However, differences in biomass between species were associated with forest type. Biomass was ranked as follows: eucalypts > ecotonal species > rainforest species (Fig. 2.1). *Backhousia myrtifolia*, however, was an exception, producing greater biomass at high irradiance. In the field, *B. myrtifolia* may be able to produce high rates of growth under high irradiance, when soil moisture and nutrient conditions are adequate.

In the second experiment, whole plant, root and leaf biomass increased in all species in response to increased irradiance from 4-6% to 21-42% sunlight (Fig. 2.4). Further increase in irradiance to 65-88% sunlight, however, produced a variable response between species. In *E. fastigata* plant biomass increased significantly even though leaf area (Fig. 2.4g) and LAR (Fig. 2.5e and 2.5f) decreased. This increase in biomass in eucalypt relative to rainforest species, may have been due to an increase in net assimilation rate under high irradiance (Hunt 1990), which itself may be due to higher

maximum rates of photosynthesis (Bjorkman 1981). Cameron (1970) showed that *E. fastigata* had a 74% increase in the maximum rate of CO_2 uptake from 15% to 42% sunlight. In contrast, Melick (1990a) observed an increase in maximum assimilation rates in *A. smithii* by only a third, from 5% to 100% sunlight. Light saturated rates of photosynthesis and acclimation to different light levels, tend to be intrinsically lower in rainforest canopy species than in those of species which regenerate at higher irradiances (Bazzaz and Picket 1980; Strauss-Debenedetti and Bazzaz 1991). However, maximal photosynthetic rates are not necessarily associated with successional status of species (Turnbull, 1991; Thompson *et al.* 1992) nor is photosynthetic acclimation between sun and shade observed in all species (eg. Langenheim *et al.* 1984; Osunkoya and Ash 1992). At 21-42% and 65-88% sunlight, biomass of different species in the second experiment, varied along a continuum (Fig. 2.4a), rather than segregating into discrete categories based on vegetation type. Rank order of biomass at high light levels in the second experiment was similar to that observed in the first experiment: *E. fastigata* > *E. sieberi* > *A. smithii* > *B. inophylla* > *C. apetalum* > *D. sassafras*. This was reversed at the lowest irradiance, where *C. apetalum* and *A. smithii* had greater biomass than both eucalypt species ($P<0.10$). Thus, relative differences in biomass gain between rainforest and eucalypt species, to light and water treatments, were similar in both experiments. Early successional or light demanding species generally have high light compensation points and high dark respiration rates, relative to shade tolerant species (Bazzaz and Picket 1980). Higher dark respiration rates and higher light compensation points in eucalypt species, may explain their lower biomass relative to *C. apetalum* and *A. smithii* at low irradiance.

The higher water treatment in both experiments increased plant biomass in eucalypt and ecotone species (Fig. 2.1b), except in *E. reticulatus* and *B. myrtifolia* in the first experiment, and *C. apetalum* in both experiments. Similarly, high nutrient treatment in the first experiment, increased total biomass in *E. sieberi, E. fastigata* and *P. undulatum* (Fig. 2.1c). It was apparent that those species which were adapted to drier, less fertile

and higher irradiance sites, may produce greater biomass, and may be competitively advantaged at higher levels of light, water and nutrient resources. Decreased biomass at low water treatment in both experiments in all species except *D. sassafras* and *C. apetalum* (Fig. 2.4b), may have been due to a limitation of photosynthesis by stomatal closure at low soil moisture (Schulze and Hall 1982). The variation in biomass in response to water treatment was lower than the response to variation in light, suggesting that light was the primary determinant of biomass gain.

Leaf area increased at high light (65-88% sunlight), water and nutrient treatments in the first experiment (Fig 2.1d, 2.1e and 2.1f) and from low to medium light treatment (4-6% vs. 21-42% sunlight), in the second experiment (Fig. 2.4). Additionally, leaf weight in the first experiment, was related to plant weight and leaf area (Fig. 2.3a and 2.3b); however, the relationships were dependent on the light environment in which the plants were grown. Greater leaf area at high treatment levels, may have resulted from a combination of increased photosynthate supply from the leaves at high light and soil moisture, and increased of nutrient uptake and the maintenance of cell turgor in expanding leaves under conditions of adequate soil moisture (Kriedemann 1986). Decreased biomass at low water and nutrient levels may be due to reduced carbohydrate supply from a lower leaf area, rather than any direct water or nutrient effects on photosynthesis (Chapin 1991). At low light, however, plant growth may be light limited, rather than limited by less photosynthetic surface area. In both experiments, plant response to light was greater than the response to water or nutrients. Increased leaf area in relation to biomass (ie. LAR) at low light levels, might be an important attribute for maintaining carbon gain in variable light environments, particularly on sheltered aspects.

Biomass partitioning.

Variation in biomass between species and treatments, may be partly explained by biomass partitioning. Although leaf area and total biomass decreased in all species at low light, the LAR increased (Fig. 2.2b and 2.5e); however, in both experiments significant differences were found only in *E. sieberi* and *E. fastigata.* Increased LAR at low irradiance increases the proportion of light harvesting structure of the plant, which may facilitate carbohydrate supply. Leaf area ratio increased even though partitioning of biomass to leaves (Fig. 2.2a) did not change between light levels. Poorter (1989) showed that LAR was highly correlated with relative growth rate (RGR). He suggested that variation in LAR may be a more important response for maintaining growth in highly variable environments, than was variation in net assimilation rate. For relatively fast growing eucalypt species, maximising leaf area under low light conditions may be essential in maintaining a high RGR (Bjorkman 1981). However, LAR of rainforest species was not significantly different between light treatments, suggesting that variation in net assimilation rate, in response to variation in irradiance, may have resulted in biomass differences between treatments (Popma and Bongers 1988; Osunkoya and Ash 1992).

Specific leaf weight, the ratio of leaf mass to leaf area, decreased significantly at low irradiance in the eucalypts (Fig. 2.2c and 2.5g), and in *C. serratifolia* and *P. undulatum* (Fig. 2.2c). *Callicoma serratifolia* is associated with gaps in disturbed rainforest canopy and the ecotone, while *P. undulatum* is generally found only in the ecotone. An increase in SLW, in response to higher irradiance, agrees with published reports for various tropical rainforest canopy species (Oberbauer and Strain 1985 and 1986; Osunkoya and Ash, 1992), pioneer species (Fetcher *et al.* 1983; Popma and Bongers 1988; Osunkoya and Ash, 1992), understorey shrubs (Denslow *et al.* 1990), northern temperate tree species (Loach 1970) and Cotton (Winter and Koniger 1991). Decreased SLW at low light was possibly due to either thinner leaves and/or lower tissue density

(Chabot and Chabot 1977; Thompson *et al.* 1988; Osunkoya 1992). Production of broader leaves for a given leaf mass at low irradiance may represent an efficient means of increasing light interception. However, broad, thin leaves might be more susceptible to herbivore and fungal disease, leading to higher mortality in shaded locations (Loach 1970; Ashton and MacCauley 1972). At high irradiance, a high SLW potentially decreases the evaporating surface area for a given amount of photosynthesizing tissue. For example, eucalypt species from arid habitats, which are subjected to high irradiance and low soil moisture, have higher SLW than those from moister habitats (Mooney *et al.* 1978). In general, those species in which SLW was not significantly different between light treatments occurred beneath the rainforest canopy and regenerate at low irradiance.

With increasing irradiance, the fraction of root biomass increased relative to leaf and stem biomass in all species. Consequently, root mass per unit leaf area and root:shoot ratio increased under high irradiance (Fig. 2.5). The largest response was observed in the two eucalypt species. Morphological and physiological plasticity has been recognised as important in increasing resource acquisition in herbs and woody shrubs (Grime *et al.* 1986). Morphological plasticity enables fast growing plants to exploit spatial and temporal variation in the availability of resources through competition. Furthermore, Schulze *et al.* (1986) suggested that interspecific competition within a canopy, may be a function of both carbon gain, which determines the amount of carbon available for partitioning, and the volume of canopy enclosed by plant structures; a more competitive species is one which occupies a greater soil and aerial volume per unit assimilated carbon. Faster growing species, such as eucalypts, increase stem height per unit stem weight, which may maximise net energy interception by overtopping other species (Givnish 1988; Rao and Singh 1989) and potentially occupy more of the canopy volume. King (1990a, 1991a and 1991b) suggested that, in temperate and tropical tree species from America, biomass allocation patterns varied between canopy and understorey species. In overstorey species, biomass was allocated in order to

increase height growth, whereas in understorey species biomass allocation tended to enhance light interception, presumably to improve survival under low irradiance. In the present work, greatest morphological plasticity between light treatments and greatest stem height per unit weight at the lowest light treatment, was observed in the two eucalypt species (Table 2.9). Morphological plasticity may be important in a variable light environment, allowing exploitation of edaphic resource pulses (Grime *et al.* 1986), and contributing to high light interception. High morphological plasticity may be advantageous in acquiring soil moisture by roots under conditions of high irradiance and variable soil moisture. Conversely, rainforest species which posses lower growth rates and reduced morphological plasticity, may maintain long term viability of leaves and roots.

Resource limitation may restrict plant growth, but biomass partitioning to root growth may reduce edaphic resource limitation. However, increased root biomass may increase carbon costs of maintenance which, under low irradiance, may reduce carbohydrate available for stem and leaf growth. These respiratory costs may increase the compensation point of the whole plant (the "ecological compensation point"; Givnish 1984 and 1988) to many times greater than the light compensation point measured by instantaneous photosynthetic rates at the leaf level. Thus, biomass partitioning between leaves and roots may represent a balance between maintaining a high leaf area, in order to supply carbohydrate for growth, but avoiding excessive shoot evaporation rates. Partitioning of biomass to root growth may increase supply of edaphic resources to leaves but at a respiratory cost.

Transpiration and water uptake.

Mean shoot evaporation rates per unit leaf area, at the end of the experimental period under different light and water treatments, were not significantly different (Fig. 2.7a

and 2.7b). The mean transpiration rate for all species and treatments was 1.75 mmol m^{-2} s^{-1}, and is within the range 0.2-2.0 mmol m^{-2} s^{-1} observed for most tropical and temperate plants (Bazzaz and Picket 1980). Similar transpiration rates between species and treatments may be due to associated variation in both stomatal control of water loss and biomass partitioning between water uptake (root) and water loss (leaf) structures, in response to different light and water treatments (Passioura 1982).

Water uptake rates varied in response to light treatment (Fig. 2.7c). At low irradiance, *E. fastigata* and *E. sieberi* had greater water uptake rates per gram root dry weight than rainforest species. Decreased rates of water uptake at medium irradiance, suggests that demand for water by shoot evaporation may have been met by increased root biomass, rather than increased root absorptivity. Caldwell and Richards (1986) and Fitter (1987) have suggested that, because availability of soil resources is predominantly dependant on soil properties, a more competitive species will maintain or increase water or nutrient uptake by growth or architectural modification of the root system, rather than by increased absorptive capacity of roots. Greater competitiveness is therefore achieved through structural adaptations. Water uptake is a function of root biomass, thus a larger root system may confer a competitive advantage over species with smaller root systems, by enabling a plant to derive greater quantities of water from a given soil volume (Schulze *et al.* 1983). In tree species, this characteristic may increase available soil moisture to seedlings until root systems are able to tap permanent sub-surface water. For example, Pereira and Kozlowski (1976) showed that a deep and ramifying root system in *Eucalyptus camaldulensis* was more effective in maintaining soil water supply and delaying the onset of water deficit, than the shallow root system of *Eucalyptus globulus*. Seedlings of eucalypt species in this study, were observed to possess larger (Fig. 2.4c and 2.4d), more ramified and finer root systems, which may be an adaptive advantage to increase extraction of water under conditions of low soil moisture and high irradiance. Smaller and less ramified root systems in rainforest

species (Fig. 2.4c), may limit water supply to leaves during periods of low rainfall, when soil moisture becomes depleted (see Chapter 5).

Plant water relations.

Plant water status responded variably to drought between species. Relatively low cell turgor occurred in both *D. sassafras* and *E. sieberi*. Bachelard (1986b) demonstrated that low turgor pressure in *E. sieberi* was a result of a low potential for osmotic adjustment in response to soil water deficits. High cell turgor, however, was maintained in *B. inophylla* and *C. apetalum* by reduction in osmotic potential. This suggests either concentration of solutes by tissue desiccation or osmotic adjustment (Morgan 1984). Osmotic adjustment may be useful in maintaining cell turgor, however, maintenance of plant growth may be independent of cell turgor (Termaat *et al.* 1985; Passioura 1988). Whatever the mechanism, it is significant that there were no obvious differences in plant water relations between vegetation types. In Australian rainforests, periodic water deficits are frequent (Doley 1986; Doley *et al.* 1987; Myers *et al.* 1987; Yates *et al.* 1988) and species may be adapted to periodic drought. It appears that the differential distribution of rainforest and eucalypt vegetation may not be dependant on responses to soil moisture alone, but rather, plant responses to the interactions between high irradiance, low humidity and low soil moisture may be important.

Implications for vegetation distribution.

The species studied in this experiment were selected as typical representatives from eucalypt, ecotone and rainforest vegetation. These species are distributed differentially along natural light, water and nutrient gradients. Typical midday measures of PAR on a horizontal surface, may be up to 2100 μmol m^{-2} s^{-1} on exposed aspects during summer

in gaps between eucalypt trees. On sheltered aspects beneath a eucalypt canopy, PAR may be reduced to 300 - 900 μmol m^{-2} s^{-1}, and beneath the rainforest canopy, PAR may be further reduced to below 50 μmol m^{-2} s^{-1}. Beneath the forest canopy, however, variability in light environment is substantial. Long periods of low irradiance are punctuated with sunflecks which provide brief periods of relatively high irradiance (Chazdon and Fetcher 1984 and 1984b; Pearcy 1987; Yates *et al.* 1988; Turton 1990). Under dense canopies, sunflecks may be the major source of light for photosynthesis (Pearcy 1988). Seedling responses to treatments in this study, may indicate potential responses in the field. However, pot trials in a glasshouse do not exactly reproduce the natural environment. While total light transmission within treatments was of the order of those experienced beneath the eucalypt forest on exposed and sheltered aspects, both spectral quality and sunfleck characteristics may be different in the forest understorey than beneath shade cloth. Additionally, soil moisture content and nutrient levels within the pots may also differ from field conditions (eg. Pereira and Kozlowski 1976), where deep soil water, lateral water and nutrient fluxes and exploitation of greater soil volumes are denied. Nevertheless, this experiment has indicated relative species responses under treatments which may be indicative of responses in the field.

Seedling growth and survival in the field in part depends on physiological responses to environmental conditions. After seed dispersal and germination, different physiological responses between species may then determine partitioning of carbohydrate into light harvesting and water and nutrient harvesting structures. Competition for resources may lead to displacement of species. Thus, a competitively superior species is one which, after successful establishment, also remains after competitive interactions have displaced inferior species (Tilman, 1987). Interspecific competitive ability is, in part, dependent on biomass accumulation (Gaudet and Keddy 1988), where rapid growth rates are likely to be advantageous (Van Andel and Biere 1989). On all aspects in open sites, eucalypts may maintain a competitive advantage over rainforest species when resources are abundant (Fig. 2.1a, 2.1b, 2.1c, 2.4a and 2.4b). Ecotonal species, such as

C. serratifolia and *P. undulatum*, however, appear to be advantaged when irradiance levels are moderate (11-20% sunlight) and moisture and nutrients are relatively high (Fig. 2.1a, 2.1b and 2.1c). Such conditions may occur near water courses beneath a eucalypt forest canopy after canopy closure, or in tree fall gaps in the rainforest canopy. Relatively higher biomass in rainforest species at low irradiance (Fig. 2.1a and 2.4a) may result in greater survival beneath the rainforest canopy. These persistent species may then be able to utilise higher light levels upon gap formation (Augspurger 1984). Establishment of ecotonal species, such as *C. serratifolia* and *P. undulatum* on sheltered aspects, may reduce irradiance at ground level and favour subsequent regeneration by more shade tolerant species. Thus, eucalypt seedlings may be out-competed by those with a tolerance to lower irradiance on sheltered aspects. Disturbance within rainforest creates higher light regimes which favour the establishment of pioneer species. However, canopy gaps in rainforest canopies may not substantially increase daily PAR at the forest floor (Chazdon and Fetcher 1984b; Osunkoya *et al.* 1992). Thus, light levels in rainforest canopy gaps on sheltered aspects in temperate regions, may be insufficient for eucalypt establishment.

Observed differences in plant biomass under the various treatments agree with the differential distribution of species along natural resource gradients: For example, eucalypts grew more at high light and occur on upper slopes where irradiance is greatest. *Callicoma serratifolia* is commonly found in moister environments associated with stream edges, while *P. undulatum* occurs on sheltered slopes. *Pittosporum undulatum* occurs as an invading species beneath eucalypt forest in Victoria and New South Wales, where it shows drought tolerance under conditions of low soil moisture, in shaded locations (Gleadow and Rowan 1982; Melick and Ashton 1991). Additionally, *P. undulatum* produced greater biomass and leaf area at 11-28% sunlight, than *E. fastigata* (Fig. 2.1a and 2.1d). This response may confer a competitive advantage to *Pittosporum* on sheltered aspects, beneath a eucalypt forest canopy. *Ceratopetalum apetalum, D. sassafras, B. inophylla, A. smithii* and *B. myrtifolia* may be

competitively advantaged over the eucalypts at low irradiance due to high biomass at less than 11-20% sunlight (Fig. 2.1a and 2.4a). However, *B. myrtifolia* and *A. smithii* were exceptional among rainforest species in their greater biomass at high light treatments (> 65% sunlight), suggesting a broad growth response to irradiance (Melick 1990a) consistent with their ability to colonise outside the rainforest canopy on relatively exposed sites.

The first hypothesis from Chapter 1, proposed that plant growth, biomass partitioning and water use characteristics would vary between rainforest and eucalypt forest species, and that these differences may enhance growth in eucalypts at high irradiance and low soil moisture, but increase growth in rainforest species under low irradiance and high soil moisture. Higher biomass under experimental treatments may result in enhanced growth rates and seedling survival in the field. In the present study, species differences in plant growth, biomass partitioning and water use were consistent with the first hypothesis. Consequently, eucalypts may be advantaged on exposed aspects by high rates of growth under high irradiance. However, slow root growth in rainforest species may be deleterious on exposed aspects, in terms of water supply for transpiration. On sheltered aspects and the gully bottom, greater biomass in rainforest species at sub-canopy light levels, may eventually create a dense canopy which excludes eucalypt species leading to a pure rainforest stand. Thus, it appears that physiological responses to environmental gradients may contribute to vegetation distribution patterns in southeastern New South Wales.

Table 2.1.

Linear regression estimates of leaf area (A, cm^2) as a function of leaf length x leaf breadth (B, cm^2) for five plants of each species harvested at the start of the experiment.

The equation is $A = b_0 + b_1 B$. The coefficients of determination (r^2) for each species and the degrees of freedom (d.f.) are indicated.

Species	r^2	d.f.	b_0	b_1
E. sieberi	0.988	49	-11.76	0.71
E. fastigata	0.985	21	-7.85	0.67
P. undulatum	0.992	78	-6.35	0.63
C. serratifolia	0.979	53	-29.40	0.67
E. reticulatus	0.970	24	-2.80	0.64
B. myrtifolia	0.982	94	-6.08	0.62
C. apetalum	0.992	33	-20.21	0.68

Table 2.2.
Summary table of the analysis of variance showing degrees of freedom (d.f.), variance ratios and their significance levels for all treatments and their interactions in the first glasshouse experiment. * significant P<0.05. ** significant P<0.01.

Source	d.f.	Variance ratio					
		Plant dry weight	Leaf area	Leaf dry weight	SLW	LAR	LWR
Light	1,12	10.46*	1.91	7.57	2.74	1.09	0.60
Water	1,17	33.84**	10.52**	21.92**	0.19	0.96	0.00
Nutrient	1,17	53.33**	25.79**	31.86**	1.12	1.78	0.01
Species	6,110	3.15**	6.55**	4.31**	4.29**	4.90**	4.92**
Light x Water	1,17	31.53**	19.05**	25.06**	1.85	2.39	0.99
Light x Nutrient	1,17	7.33*	1.68	3.38	0.22	0.58	0.34
Light x Species	6,110	16.04**	5.30**	12.01**	8.72**	10.80**	1.81
Water x Nutrient	1,17	21.96**	6.31*	14.00**	1.70	1.29	0.02
Water x Species	6,110	4.89**	5.17**	5.33**	0.41	0.42	2.97*
Nutrient x Species	6,110	6.44**	4.62**	5.90**	0.28	0.85	1.77
Light x Water x Nutrient	1,17	1.23	1.87	1.23	0.01	0.25	0.34
Light x Water x Species	6,110	2.89*	2.78*	3.03**	1.02	0.75	2.11
Light x Species x Nutrient	6,110	0.46	1.37	0.66	1.34	0.84	1.69
Species x Water x Nutrient	6,110	1.02	2.71	1.18	1.79	4.70**	4.96**
Light x Species x Water x Nutrient	6,110	3.05*	1.44	2.43*	0.99	1.77	0.88

Table 2.3.
Mean values for the two-way interaction terms in the analysis of variance of plant dry weight (g), leaf area (cm^2) and leaf dry weight (g) in the first glasshouse experiment. Mean values are adjusted for the covariate. s.e.d. = standard error of the difference of means.

	Mean values				
Light x water	High light		Low light		s.e.d.
	High water	Low water	High water	Low water	
Plant dry weight	3.88	2.75	0.65	0.64	1.36
Leaf area	121.15	82.19	31.03	32.56	1.46
Leaf dry weight	1.95	1.34	0.33	0.33	1.44
Light x nutrient	High light		Low light		s.e.d.
	High nutrient	Low nutrient	High nutrient	Low nutrient	
Plant dry weight	3.80	2.81	0.69	0.61	1.37
Leaf area	117.45	84.77	34.78	29.08	1.69
Leaf dry weight	1.87	1.40	0.35	0.31	1.44
Water x nutrient	High water		Low water		s.e.d.
	High nutrient	Low nutrient	High nutrient	Low nutrient	
Plant dry weight	1.90	1.34	1.38	1.28	1.04
Leaf area	74.07	50.75	55.09	48.52	1.07
Leaf dry weight	0.95	0.67	0.69	0.64	1.06

Table 2.4.

Summary table showing variance ratios for the analysis of variance of growth parameters, treatments and interaction terms for four rainforest and two eucalypt species in the second glasshouse experiment. d.f. = degrees of freedom. * significant $P<0.05$; **significant $P<0.01$.

Source	d.f.	Variance ratio			
		Biomass	Root dry weight	Leaf dry weight	Leaf area
Light	2,4	118.39**	124.99**	83.88**	41.49**
Water	2,12	16.02**	13.09**	17.23**	16.37**
Species	5,72	10.96**	15.34**	5.96**	17.75**
Light x Water	4,12	0.45	1.28	0.33	0.22
Light x Species	10,72	15.78**	11.86**	9.87**	3.46**
Water x Species	10,72	2.36*	2.02*	1.75	0.96
Light x Water x Species	20,72	1.44	0.92	1.04	1.27

Table 2.5.

Mean fraction of biomass allocated to stems, roots and leaves in two eucalypt and four rainforest species from southeastern New South Wales, grown for 17 weeks in three light and three water treatments. s.e.d. = standard error of difference of means. * significant $P<0.05$, ** signficant $P<0.01$. N.S. = not significant.

Treatment	Root fraction	Stem fraction	Leaf fraction
Light			
65 - 88%	0.29	0.23	0.47
21 - 42%	0.27	0.24	0.48
4 - 6%	0.21	0.27	0.52
s.e.d.	0.01	0.01	0.01
significance	**	*	*
Water			
110 ml	0.26	0.25	0.49
70 ml	0.24	0.25	0.50
35 ml	0.27	0.25	0.48
s.e.d.	0.01	0.01	0.02
significance	*	N.S.	N.S.

Table 2.6.
Summary table of variance ratios for the analysis of variance of all biomass partitioning parameters, treatments and interaction terms for two rainforest and four eucalypt species in the second experiment. d.f. = degrees of freedom. * significant P<0.05, ** significant P<0.01.

Source	d.f.	Variance ratio					
		Root: shoot	Root mass: leaf area	Leaf weight ratio	Leaf area ratio	Specific leaf weight	Stem height: weight
Light	2,4	43.97**	69.27**	14.75**	99.46**	15.43*	742.14**
Water	2,12	4.85*	1.61	1.34	1.72	1.79	24.54**
Species	5,74	5.88**	5.84**	5.38**	32.99**	7.86**	139.94**
Light x Water	4,12	1.18	0.55	0.69	3.89*	2.21	12.03**
Light x Species	10,74	92.03*	1.93	1.51	15.63**	2.99**	106.71**
Water x Species	10,74	0.79	1.94	0.30	1.55	0.86	33.18**
Light x Water x Species	20,74	0.44	0.99	0.40	2.46*	0.85	33.71**

Table 2.7.
Summary table of variance ratios for the analysis of variance of water use parameters, treatments and interaction terms for two rainforest and four eucalypt species in the second glasshouse experiment. d.f. = degrees of freedom.
* significant P<0.05, ** significant P<0.01.

Source	d.f.	Variance ratio	
		Shoot transpiration rate	Water uptake rate
Light	2,4	0.37	9.74*
Water	2,12	0.98	3.25
Species	5,64	0.82	6.01**
Light x Water	4,12	1.18	1.06
Light x Species	10,64	1.80	4.37**
Water x Species	10,64	1.33	0.77
Light x Water x Species	20,64	1.32	1.49

Table 2.8.

Mean leaf tissue water potential (Ψ, MPa), osmotic potential (π, MPa), turgor pressure (P, MPa), succulence ($g_{H_2O}\ m^{-2}$) and relative water content ($g_{H_2O}\ g^{-1}$ leaf dry weight) for two eucalypt and four rainforest species from southeastern New South Wales, subjected to soil mositure deficit after 17 weeks growth under three light and three water treatments.

Species	Ψ	π	P	Succulence	Relative water content
Eucalyptus sieberi	-1.88	-2.25	0.37	68.6	189.9
Eucalyptus fastigata	-0.93	-1.83	0.90	69.9	230.3
Acmena smithii	-0.73	-1.97	1.24	84.3	179.5
Baloghia inophylla	-0.43	-2.23	1.80	100.6	231.2
Doryphora sassafras	-1.30	-1.87	0.57	119.2	312.3
Ceratopetalum apetalum	-0.63	-2.51	1.88	100.7	219.3
s.e.d.	0.19	0.17	0.25	6.8	24.3

Table 2.9.
Summary of relative responses by rainforest and eucalypt forest species to experimental treatments.

Measured parameter	Eucalypt species	Rainforest species
Total biomass	Responsive to resource availability	Limited response to resource availability.
Growth rate	High at high resource availability	Low at all resource availabilities
Leaf area	Variable, responsive to resource availability	Limited response to resource availability.
Root biomass	Responsive to resource availability	Limited response to resource availability.
Root architecture	Fibrous, occupying most of pot volume	Less ramified and stout, usually limited to upper soil layers in pot
Leaf weight ratio	Not responsive to experimental treatments	
Leaf area ratio	Increased at low irradiance	Limited response to treatments
Specific leaf weight	Increased at high irradiance	Limited response to treatments
Root:Shoot mass	Increased at high irradiance	
Root mass:Leaf area	Increased at high irradiance	
Stem height:Stem mass	Decreased at high irradiance	Limited response to treatments
Transpiration rate	No consistant differences between species under experimental treatments	
Water uptake rate per unit root mass	Increased at low irradiance	Limited response to treatments
Water relations	No consistant differences between species under experimental treatments	

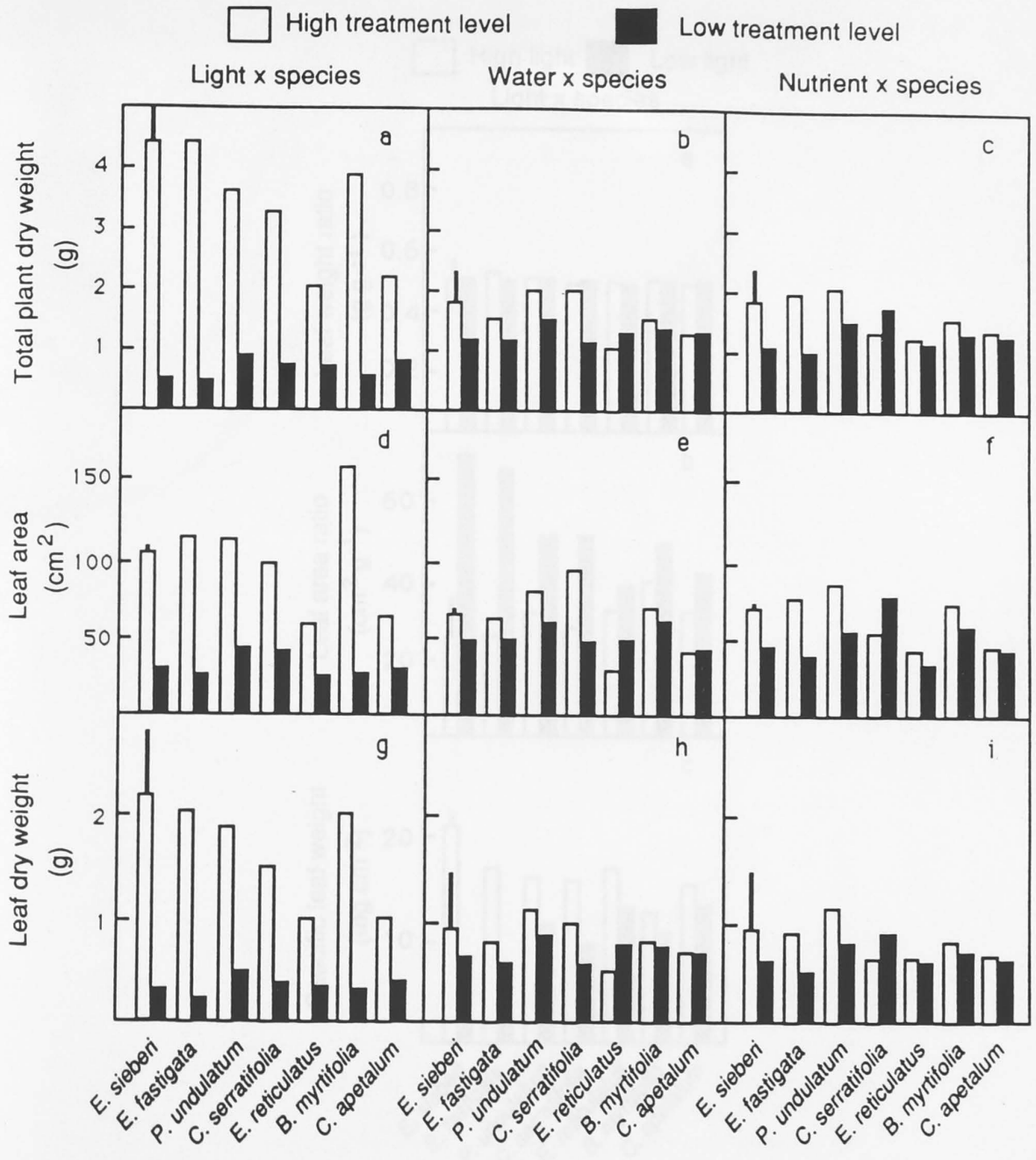


Figure 2.1. Bar charts of mean total plant dry weight, leaf area, and leaf dry weight, adjusted for the covariate, for two-way interaction terms of Light x Species (a, d, g), Water x Species (b, e, h) and Nutrient x Species (c, f, i) in the analysis of variance. The vertical bar represents the standard error of the difference of means adjusted for the covariate.

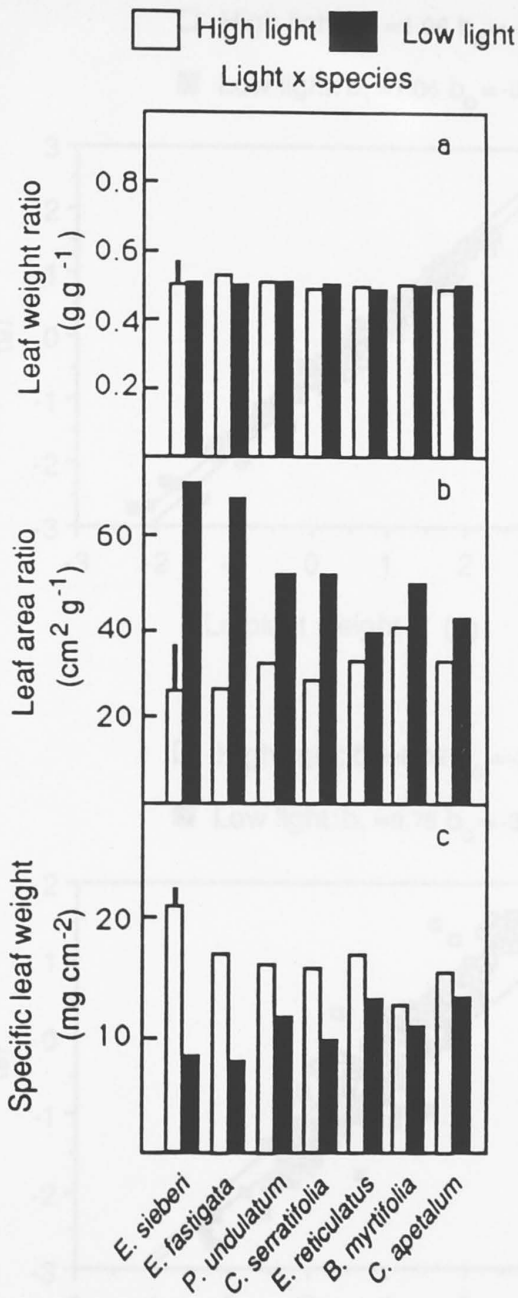


Figure 2.2. Bar charts of (a) leaf weight ratio, (b) leaf area ratio and (c) specific leaf weight for the Light x Species interaction in the analysis of variance. The vertical bar represents the standard error of the difference of means.

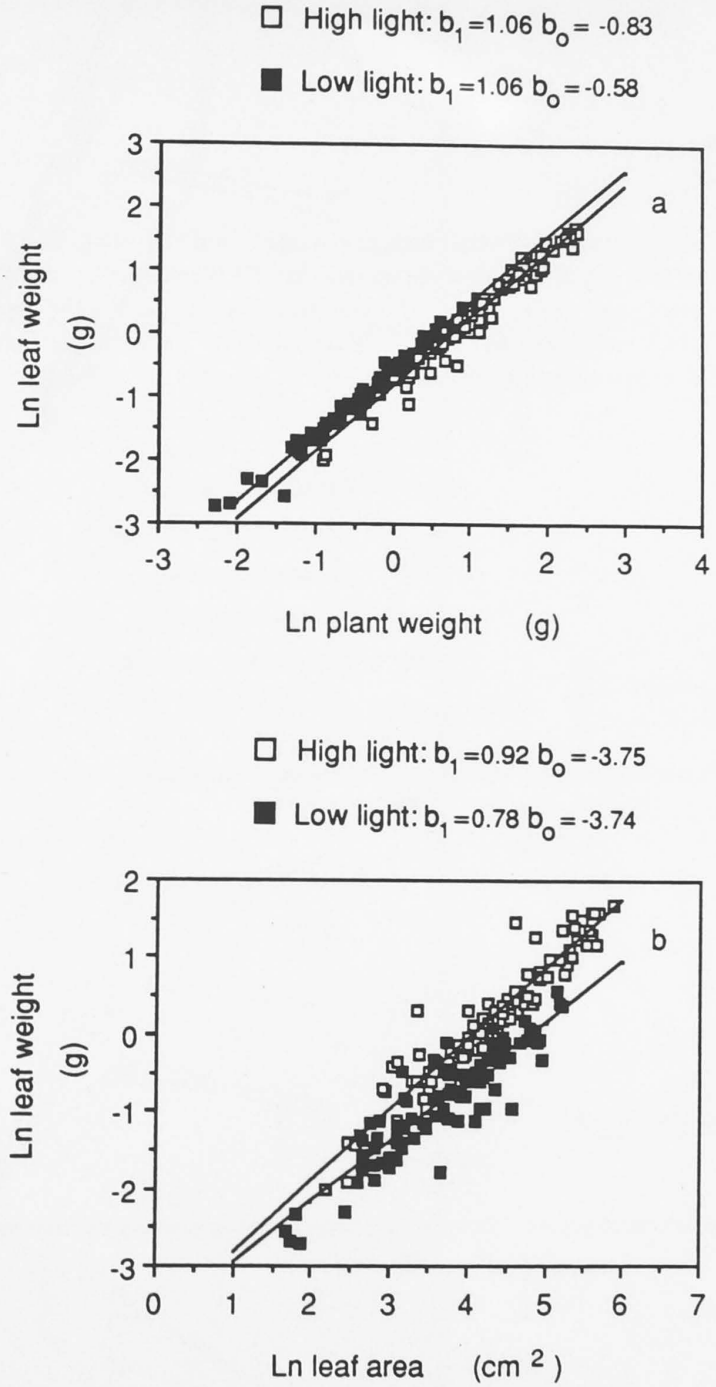
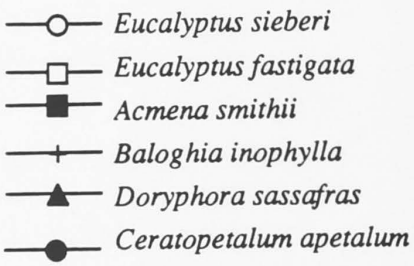


Figure 2.3. Leaf weight as a function of (a) plant weight and (b) leaf area for all plants of all seven species in the first glasshouse experiment. Open symbols represent high light treatment and closed symbols represent low light treatment. Least squares regression lines were fitted with slopes (b_1) and y-intercepts (b_o). Slopes do not differ significantly for plant weight. Y-intercepts do not differ significantly for leaf area.

Figure 2.4. Mean plant biomass, root dry weight, leaf dry weight and leaf area for two eucalypt and four rainforest species grown for 17 weeks under combinations of three light and three water treatments. The middle value of each light treatment is used in plots depicting responses to light. Vertical bars indicate standard errors of the difference of means between treatments.



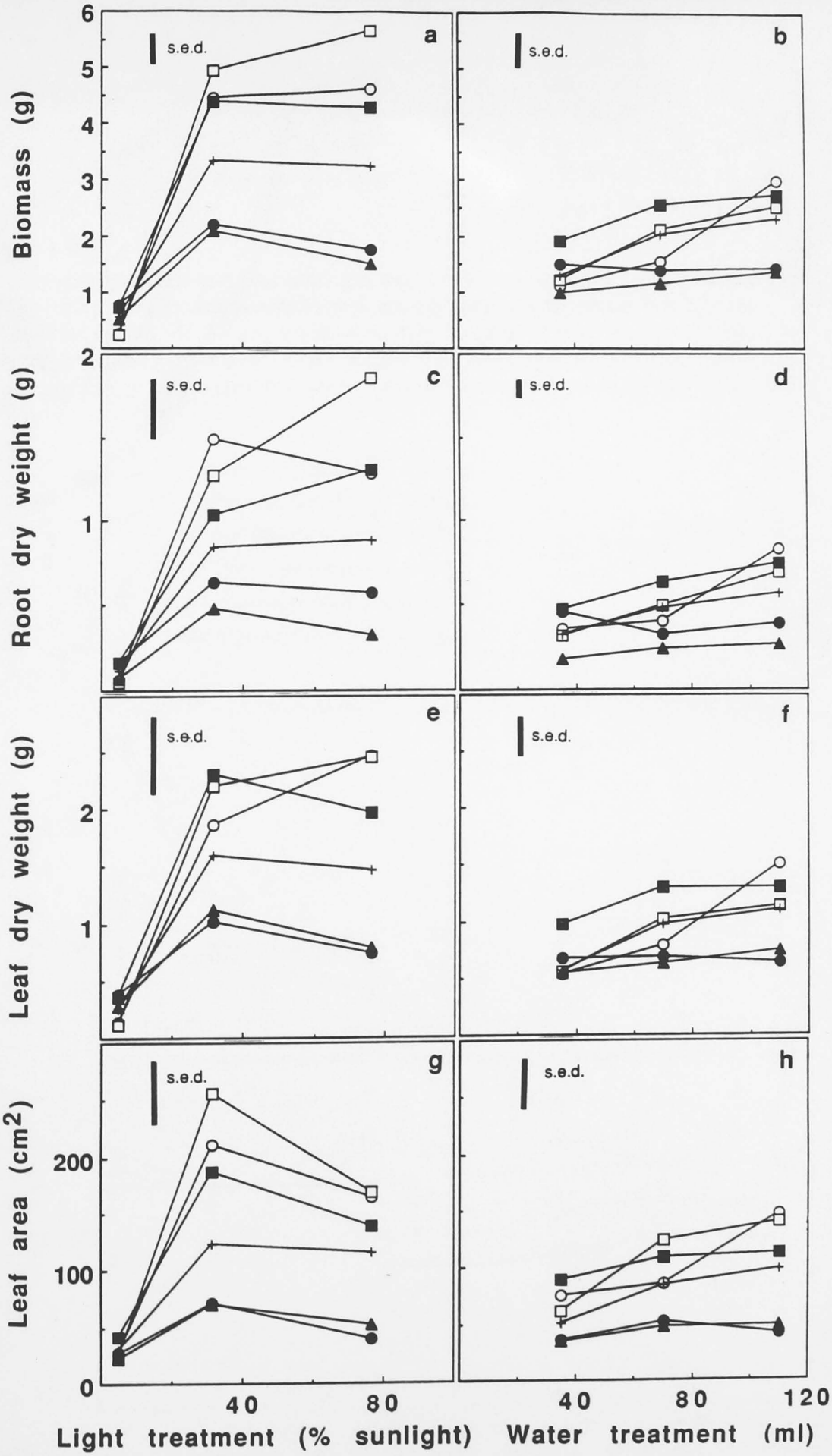
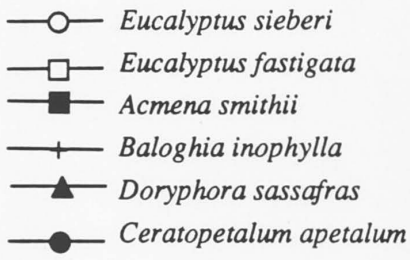
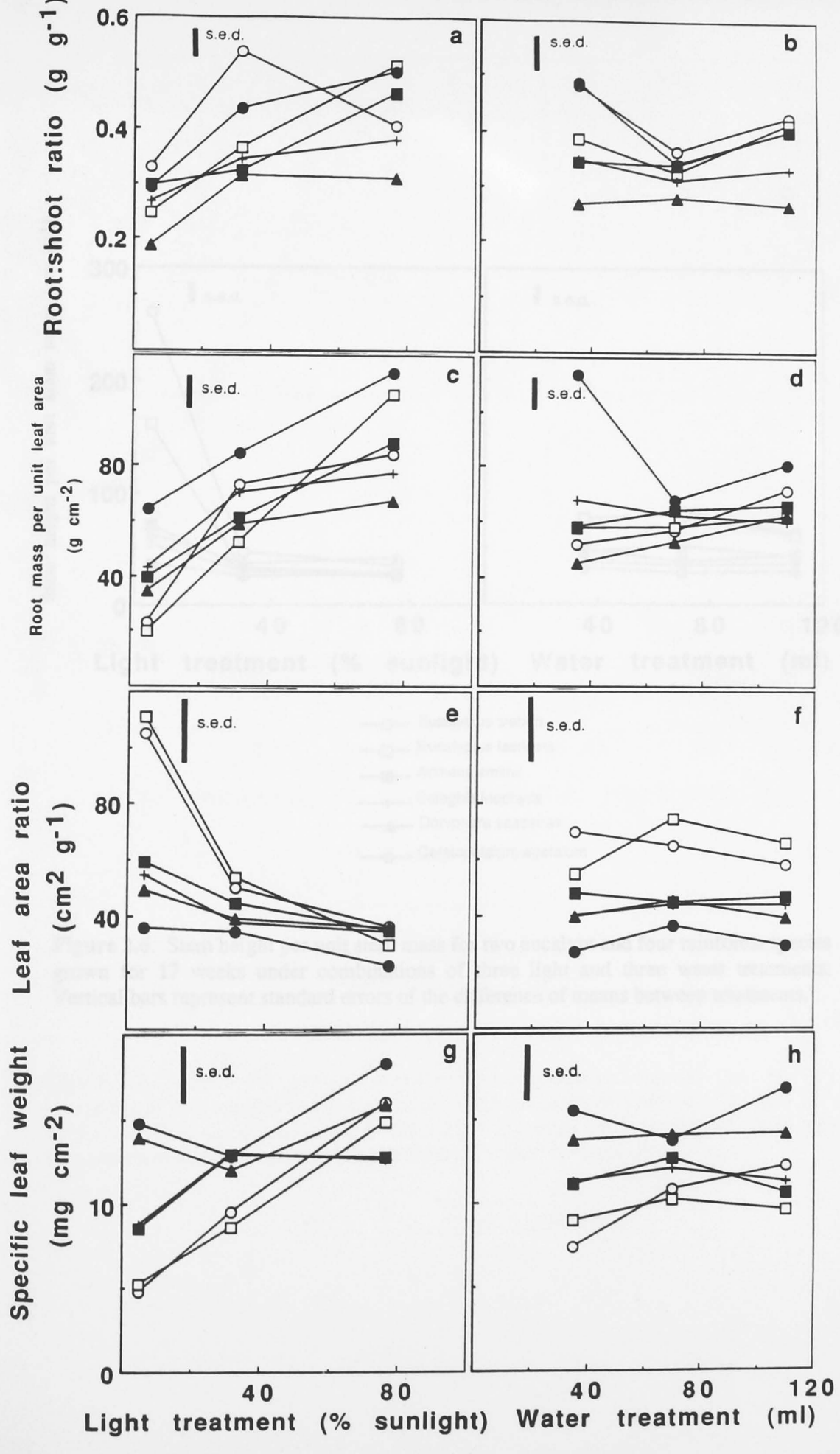

Biomass (g)
Root dry weight (g)
Leaf dry weight (g)
Leaf area (cm2)
s.e.d.
a
b
c
d
e
f
g
h
0
100
200
1
2
3
4
5
6
40
80
120
Light treatment (% sunlight)
Water treatment (ml)

Figure 2.5. Mean root:shoot ratio, root mass per unit leaf area, leaf area ratio and specific leaf weight for two eucalypt and four rainforest species grown for 17 weeks under combinations of three light and three water treatments. The middle value of each light treatment is used in plots depicting responses to light. Vertical bars represent standard errors of the difference of means between treatments.




Root:shoot ratio (g g-1)
Root mass per unit leaf area (g cm-2)
Leaf area ratio (cm2 g-1)
Specific leaf weight (mg cm-2)
s.e.d.
a
b
c
d
e
f
g
h
0.6
0.4
0.2
80
40
80
40
10
0
40
80
40
80
120
Light treatment (% sunlight)
Water treatment (ml)

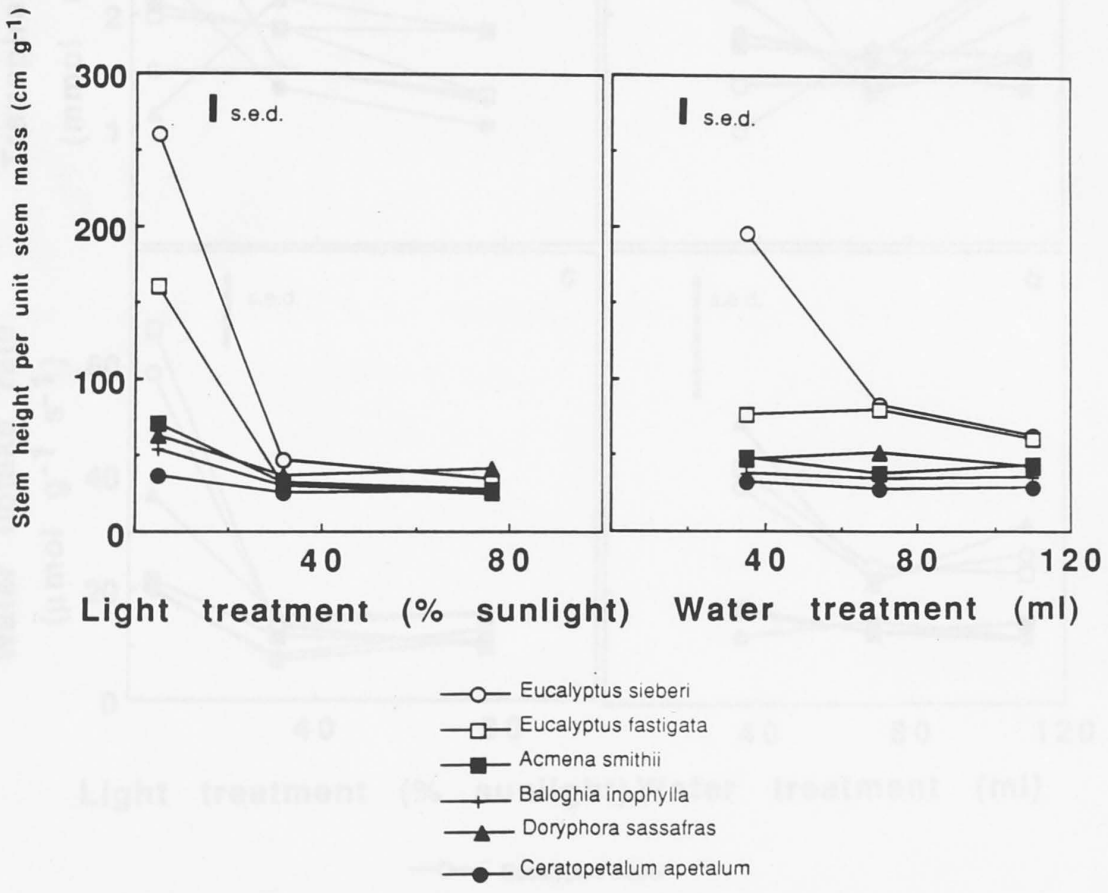


Figure 2.6. Stem height per unit stem mass for two eucalypt and four rainforest species grown for 17 weeks under combinations of three light and three water treatments. Vertical bars represent standard errors of the difference of means between treatments.

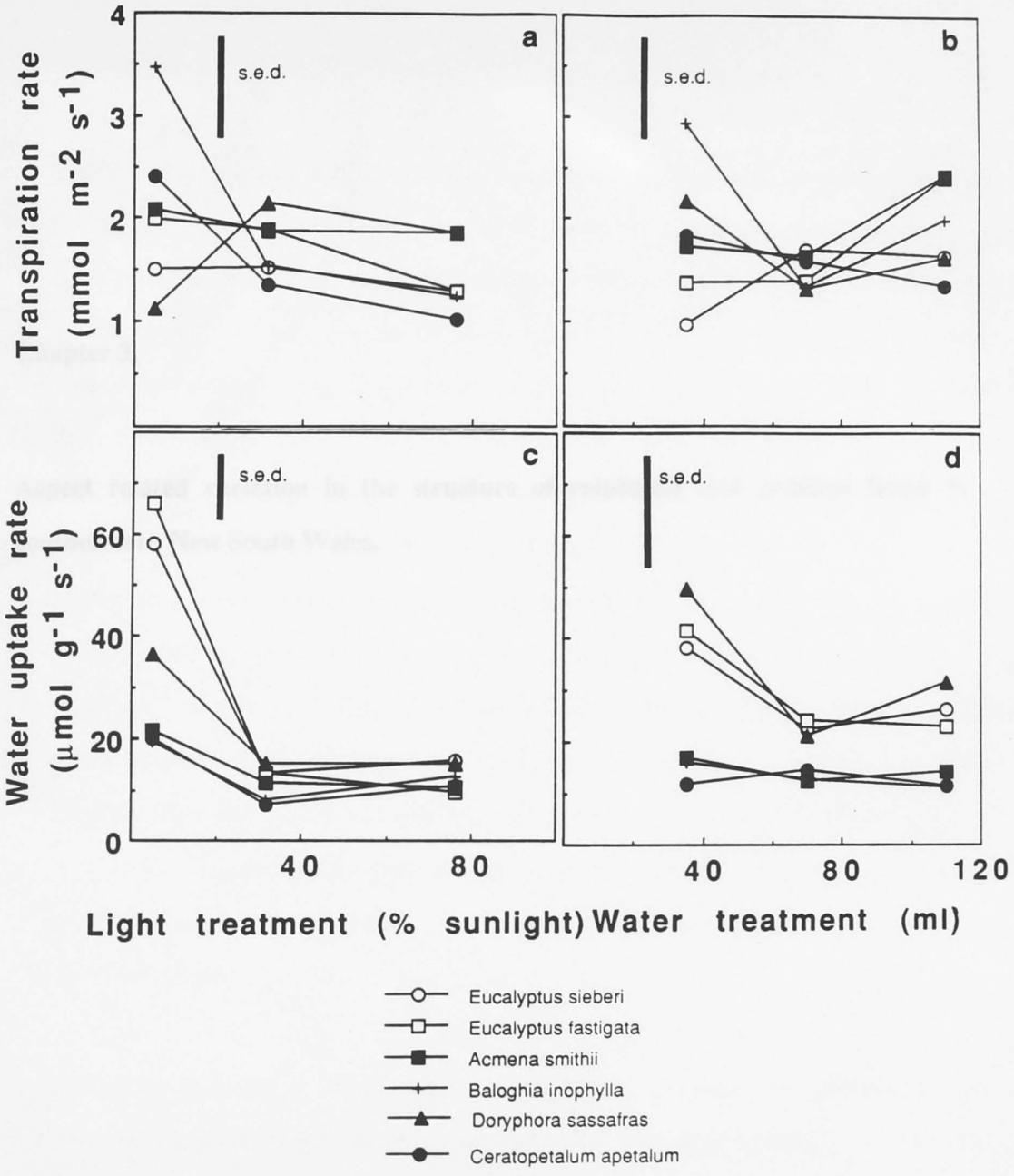


Figure 2.7. Mean shoot evaporation rate and water uptake per unit root mass in two eucalypt and four rainforest species one day after watering to field capacity after 17 weeks growth under combinations of three light and three water treatments. Vertical bars represent standard errors of the difference of means between treatments.

Chapter 3.

Aspect related variation in the structure of rainforest and eucalypt forest in southeastern New South Wales.

Abstract

Canopy structure and tree characteristics were investigated in rainforest and eucalypt forest on exposed and sheltered aspects, in a forested catchment in southeastern New South Wales. Plant area index, estimated by hemispherical photographic techniques, varied between forest types and between seasons. Mean plant area index in rainforest plots was greater than in eucalypt forest plots. In the rainforest canopy, plant area index varied between 2.9 and 4.3, whereas in eucalypt forest, plant area index varied between 2.1 and 3.2. The major component of plant area index was leaf area, thus variation in plant area index was attributed to seasonal variation in canopy leaf area. However, the hemispherical photographic technique may be subject to bias caused by the effect of photographic exposure on image intensity on the film and by the relationship between pixel size and canopy height. The bias associated with photographic exposure was particularly evident in eucalypt forest where high leaf reflectivities and flaring of light around leaves and stems, removes leaf area from the image at low zenith angles (ie. overhead). Consequently, estimates of plant area index using the hemispherical photographic technique need to be calibrated against independent measurements for each forest type.

Mean tree diameter at breast height (dbh), crown area and tree biomass on four experimental plots, were greater in eucalypt forest trees than in rainforest. However, within a forest type no topography related differences in tree characteristics were evident. In rainforest trees, crown area was more extensive per unit biomass than in eucalypt trees. Greater crown area per unit biomass may facilitate interception of irradiance particularly in canopies with high leaf area index, and may contribute to competitive shading of light demanding species such as eucalypts. Conversely, a less extensive crown area per unit biomass in conjunction with a low leaf area index, may reduce radiation interception per tree under high irradiances. Thus, eucalypt forests, which occupy ridge tops and exposed aspects, are characterised by relatively large trees,

of greater biomass and possessing more expansive crowns, but with lower leaf area indices, than rainforest trees which occupy sheltered aspects and the gully bottom.

Introduction

The distribution and orientation of leaves within a forest canopy influences radiation interception, which itself may determine leaf energy balance (eg. Miller 1967; Caldwell *et al.* 1986), the temperature and humidity of the air near the canopy, and canopy transpiration (Jarvis 1981; McNaughton and Jarvis 1983 and 1991). Additionally, canopy structure profoundly influences the microenvironment of the understorey by intercepting radiation (Anderson 1970; Ross 1981; Oker-Blom and Kellomaki 1983; Baldocchi *et al.* 1985; Campbell and Norman 1989). Variation in canopy leaf temperature directly affects transpiration by determining the water vapour concentration gradient between leaves and the atmosphere. Thus, differences in leaf area and orientation between rainforest and eucalypt forest canopies may result in differences in water use characteristics between forest types. On natural light and water gradients, such as occurs in southeastern New South Wales, different water use strategies between species may be important in determining vegetation distribution patterns.

Cursory field observation indicated differences in canopy structure and vegetation characteristics between rainforest and eucalypt forest. It was obvious that eucalypt forest canopies had lower light interception and were composed of leaves at steeper inclination angles, than rainforest canopies. Canopy leaf area in many vegetation types has been related to availability of soil moisture (Grier and Running 1977; Specht and Morgan 1981; Gholz 1982; Waring 1983; Specht 1983). Indeed, Pook (1985) showed that leaf area index in *Eucalyptus maculata* forest decreased in response to severe drought and recovered when soil moisture increased. Therefore, higher leaf area indices may be expected in locations of higher soil moisture, such as on sheltered

aspects and gully bottoms. In addition, field observation indicated greater tree height, stem diameter and crown area per tree in eucalypt forest than in rainforest. Lower soil moisture may reduce growth, thereby limiting forest biomass production in many species (Waring and Franklin 1979; Gholz 1982; Whitehead *et al.* 1984; Waring 1983; Price and Black 1991). Therefore, lower forest biomass may be expected on exposed aspects and upslope sites, than on sheltered aspects and the gully bottom, because of differences in soil moisture content (eg. Becker *et al.* 1988).

The first aim of this chapter is to quantify the apparent differences in canopy structure between rainforest and eucalypt forest, at a field site in southeastern New South Wales. Steep terrain throughout the region prevented direct access to the canopy. Consequently, hemispherical canopy photography, using the procedure of Norman and Campbell (1989), was used to estimate plant area index of the canopy. The second hypothesis (Chapter 1) proposed that differences in water use characteristics are manifest as differences in canopy structure between vegetation types. In order to determine the relationships between canopy structure and transpiration, canopy photographs were taken in conjunction with sap flow measurements (see Chapter 5) at different times of the year. However, a number of problems were encountered using this technique which are discussed in detail in this chapter. The second aim of this chapter is to quantify the tree diameter, sapwood area and biomass of eight selected rainforest and eucalypt forest trees used in Chapter 5, on each experimental plot at the field site.

Photographic measurement of canopy structure.

Hemispherical photography is a useful technique to quantify plant area index (L_O) under conditions where direct access to the canopy is difficult, such as in tall forests in rugged terrain. Plant area index of forest canopies includes leaf, stem and branch areas,

thus leaf area index is a fraction of the plant area index. Warren-Wilson (1959, 1960 and 1965) showed that the plant area index of a canopy was proportional to the mean number of contacts between foliage elements and a thin probe (a "point quadrat") passed at various angles through a canopy. Reeves (in the appendix to Warren-Wilson 1960) related the number of contacts by the point quadrat to the angular distribution of leaf inclination and the insertion angle of the probe. In a similar derivation, Philip (1965) derived plant area index from contact frequency data, in a lucerne crop. However, the height of forest canopies prevents the use of a physical point quadrat. Instead, the transmittance of a light beam is used as a "probe"; Warren-Wilson's contact frequency is replaced by the negative natural logarithm of either the gap fraction estimated from hemispherical photographs (Norman and Campbell 1989; Neumann *et al.* 1989; Chen *et al.* 1991) or the transmittance of the direct solar beam (Lang 1986; Lang and Xiang 1986; Lang 1987 and 1991). The gap fraction is the proportion of gap per unit area of projected canopy.

Theory.

For a canopy where the projection of foliage elements is randomly distributed on the projection plane, the probability of a light beam intersecting a foliage element is dependant on the beam zenith angle and the foliage inclination angle, and is described by a Poisson distribution. The probability of the beam encountering no foliage (ie. a gap) is:

$$P(\theta) = e^{\left(\frac{-G(\theta)L_o}{\cos\theta}\right)} = e^{(-K(\theta)L_o)} \qquad (3.1)$$

where $P(\theta)$ is the probability of a beam of zenith angle, θ, not encountering any foliage, $G(\theta)$ is the leaf orientation function, $K(\theta)$ is the canopy extinction coefficient and L_o is the plant area index of the canopy (Harper 1987; Campbell and Norman 1989; Chen *et*

al. 1991). The leaf orientation function ($G(\theta)$) is the proportion of foliage area projected on a plane normal to a beam passing through a canopy (Ross 1981). It describes the relationship between effective foliage area and foliage orientation for a given beam direction. The leaf orientation function is related to the extinction coefficient ($K(\theta)$, Warren-Wilson 1959, 1965) of a canopy by,

$$K(\theta) = \frac{G(\theta)}{\cos \theta} \qquad (3.2)$$

The relationship between both $G(\theta)$ and the transfer of light through the canopy provides the basis for estimating canopy structure using hemispherical photographs.

A hemispherical photograph of the sky represents all zenith angles, θ, as radial distances on a flat plane. Thus in a distortion free lens, objects at $\theta = 0^o$ have a radius of 0 r, those at $\theta = 45^o$ are 0.7 r and $\theta = 90^o$ are 1.0 r; where r is the radius of the image. In this way the zenith and azimuth angle (θ,ξ) of any point in a canopy may be determined from the radius and azimuth of that point on the photograph. In a uniform forest canopy, the proportion of gap for any region centred on the zenith angle, θ, summed over all azimuth angles, is equivalent to $P(\theta)$. Hence, canopy gap measurements derived from hemispherical photographs, may be used to determine canopy plant area index, L_o (Norman and Campbell 1989 and summarised by Perry *et al.* 1988; Neumann *et al.* 1989 and Chen *et al.* 1991).

If we define $T(\theta)$ as the proportion of gap in a unit area (ie. the gap fraction), centred at a zenith angle, θ, on a hemispherical photograph then:

$$T(\theta) = P(\theta)$$

$$T(\theta) = e^{\left(\frac{-G(\theta)L_o}{\cos \theta}\right)} = e^{(-K(\theta)\, L_o)}.$$

$$\text{Therefore, } -\ln T(\theta) = \frac{G(\theta)L_o}{\cos\theta} = K(\theta)L_o. \qquad (3.3)$$

The functions G and K vary with zenith angle (Ross 1981), therefore equation (3.3) must be considered for all zenith angles by dividing the hemispherical photograph into a series of i zenith angle classes where $i = 1, 2, \ldots, m$. Additionally, G and K vary with foliage inclination angle, therefore equation (3.3) must be considered for j leaf inclination classes where $j = 1, 2, \ldots, n$. The probability of a canopy gap may then be calculated from the product of the probabilities of a light beam penetrating each leaf inclination angle class for each zenith angle class (Campbell and Norman 1989). Hence equation (3.3) becomes:

$$-\ln T(\theta) = \Sigma\, K(\theta_i\, \alpha_j)\; L_j, \text{ so}$$

$$-\ln T(\theta) = K(\theta_1\, \alpha_1)L_1 + K(\theta_1\, \alpha_2)L_2 + \ldots + K(\theta_m\, \alpha_n)L_n \qquad (3.4)$$

which is a linear function whereby the leaf area index for the jth leaf angle class, L_j, can be solved by least squares when $T(\theta_i)$ and $K(\theta_i\ \alpha_j)$ are known (Norman and Campbell, 1989; Campbell and Norman 1989; Neuman *et al.* 1989. Chen *et al.* 1991). $K(\theta_i\ \alpha_j)$ is the extinction coefficient of a light beam of zenith angle, θ_i, and leaf inclination class, α_j, and is determined from a mathematical model of leaf distribution within the canopy. Commonly, the spherical leaf angle distribution is used since many canopies approximate this (Ross 1981). This model assumes that leaf azimuth angles are equally orientated in all directions, that canopy foliage elements are randomly distributed in space and that the canopy is horizontally homogeneous.

The least squares solution for L_j, using the "inversion technique" of Norman and Campbell (1989) is,

$$\mathbf{L} = (\mathbf{K}^{\mathbf{T}}\ \mathbf{K})^{-1}\ (\mathbf{K}^{\mathbf{T}}\ \mathbf{T}) \qquad (3.5)$$

Where the natural logarithm of the gap fraction for each zenith class, *i*, is

$$\mathbf{T} = \begin{pmatrix} -\ln T(\theta_1) \\ -\ln T(\theta_2) \\ -\ln T(\theta_3) \\ . \\ . \\ . \\ -\ln T(\theta_m) \end{pmatrix}$$

K is used as a kernel matrix and $\mathbf{K}^{\mathbf{T}}$ is its transpose,

$$\mathbf{K} = \begin{pmatrix} K_{1\,1}\, K_{1\,2} \ldots K_{1\,m} \\ K_{2\,1}\, K_{2\,2} \ldots K_{2\,m} \\ . \quad . \quad \ldots \quad . \\ . \quad . \quad \ldots \quad . \\ K_{n\,1}\, K_{n\,2} \ldots K_{n\,m} \end{pmatrix}$$

where, for a canopy with a spherical foliage angle distribution,

$$K(\theta_i\ \alpha_j) = \begin{cases} \cos \alpha_j & \text{if } 0 <= \frac{\pi}{2} - \alpha \\ \cos \alpha_j\ 1 + \frac{2\,(\tan x - x)}{\pi} & \text{if } 0 > \frac{\pi}{2} - \alpha \end{cases}$$

where $x = \cos^{-1}(\cot \alpha_j \cot \theta_i)$,

The plant area index matrix for each leaf angle class, α_j, *is*

$$\mathbf{L} = \begin{pmatrix} L_1 \\ L_2 \\ . \\ . \\ . \\ L_n \end{pmatrix}$$

and the total plant area index, $L_o = L_1 + L_2 + ...+ L_n$ (3.6)

Hence, assuming that the projection of foliage on the projection plane is random, an estimate of plant area index may be obtained from information on the proportion of canopy gap at various zenith angles.

Methods

Study site.

A field site was chosen on the basis of several criteria: (a) it should contain a relatively extensive and floristically diverse temperate rainforest and eucalypt forest typical of the region, (b) it was relatively undisturbed by logging or fire, (c) the orientation of the catchment was such that opposing slopes were predominantly exposed (north facing) and sheltered (south facing), in order to compare maximum contrast between aspects, and (d) it was located close to laboratory facilities and was accessible by roads. The field site was located in part of the Kioloa Flora Preserve on Union Camp Creek (35° 35'S, 150° 20'E, altitude 50 - 285 m), 1.25 - 2.5 km inland from the Pacific Ocean, on the northwestern side of Durras Mountain, and 5.2 km south of the Australian National University, Edith and Joy London Foundation, research station. This forest was classified by Floyd (1990a and 1990b) as the southernmost example of the *Ceratopetalum-Diploglottis australia-Acmena smithii* suballiance, in which several tree

species, such as *D. australis, Diospyros pentamera* and the palm *Archontophoenix cunninghamiana* reach their southern limit.

With assistance from undergraduate students, the distribution of different vegetation types in the catchment was determined by measuring the ground surface distance from ridge top to the boundary of each vegetation type on 21 transects positioned across the catchment (Fig. 3.1). Three vegetation types were identified on the basis of species composition, tree size and canopy characteristics (Yates 1989; Ash and Helman 1990): (a) Eucalypt forest was characterised by *Eucalyptus maculata* and *Eucalyptus pilularis* with variable development of an understorey of *Acacia mabelliae*, (b) rainforest, dominated by *Doryphora sassafras, Ceratopetalum apetalum, Cryptocarya microneura, Acmena smithii, Backhousia myrtifolia* and *Archontophoenix cunninghamiana*, and, (c) ecotonal vegetation characterised by the presence of notophyll species beneath a eucalypt overstorey, typically with the presence of *Elaeocarpus reticulatus, Tristania laurina, Tasmania lanceolata, Synoum glandulosum, Callicoma serratifolia, Pittosporum undulatum* and *Acacia mabelliae*.

Four 30 x 30 m plots were located along a single transect of 220° azimuth which traversed the catchment (Fig. 3.1). On the sheltered aspect, plots were centred at distances of 45 m and 129 m from the northern ridge top in eucalypt forest and rainforest, respectively. On the exposed aspect, plots were centred at distances of 80 m and 228 m from the southern ridge top, again in eucalypt forest and rainforest, respectively. All four plots were located close to boundaries between forest types. However, plots on the sheltered aspect were higher upslope than on the exposed aspect because of the assymetrical distribution of forest on different aspects. Slope angle varied considerably between plots. Mean slope angle, derived from three measures on each plot, ranged from 28° on the sheltered aspect rainforest site, to 7° to 12° on other plots (Table 3.1).

Plant area index.

In July and November 1991, and March 1992, hemispherical canopy photographs were taken on each of the four plots at the field site using a Cannon 7.5 mm fish-eye lens on a Cannon AV-1 aperture priority automatic camera, and Agfa Pan 100 ASA film. This lens was distortion free at angles up to $\theta = 40^{o}$ (ie. 0.6r), with maximum distortion of 8% at $\theta = 53^{o}$ (ie. 0.8r; Fig 3.2). The camera was levelled using two spirit levels fixed at right angles to the camera body and the sides of the frame were orientated true north-south using a prismatic compass. Three photographs were taken at each of five positions on the four plots. Exposure for the first photograph was determined by the camera's automatic metering system with aperture set at f/11, and two other photographs were taken at one stop over and one stop under-exposure, resulting in a doubling and halving of exposure, respectively. Shutter speed in all cases was < 1 second. The clearest definition of the canopy was achieved in the absence of direct sunlight and at low wind speeds so that leaf shake was minimised (Anderson 1981; Harper 1987; Rich 1989). In winter, photographs were taken before sunrise or after sunset, whereas in early summer and autumn photographs were taken during overcast conditions. It was found that overcast conditions gave the most even distribution of light necessary to discriminate between foliage and sky. Some photographs taken in winter shortly before sunrise, were unsuitable because of the brightness of the sky in the region around the sun, even when the solar disc was below the horizon. Under these conditions, the range of tones across the sky presented difficulties in estimating the gap fraction of the canopy. Because of the problems associated with the winter photographs, only two photographs on both southern aspect sites in winter were available for analysis. At all other times, 5 photographs per site were used to calculate plant area index.

The film was developed using standard developing procedure in Ilford developer and then printed to a picture diamter of 17.5 cm on Agfa multigrade paper, using the

minimum exposure time necessary to print the foliage as black. Photographs were inspected for eveness of sky tone, maximum contrast between sky and foliage, minimum flaring of light in gaps and focus. Exposures using the automatic meter within the camera were found to best fit the above criteria. Measurement of gap fraction from the photographic image was achieved in two stages: Firstly, the photograph was aligned on a light box then digitised using an image analysis system (Skye Instruments, Powys, U.K.) linked to an IBM compatible personal computer. The image was stored as a 640 x 325 x 8-bit array with a pixel intensity between 0 (Black) and 255 (white) assigned to each pixel. The image was saved to disc as an ASCII file. Secondly, the digitised image was automatically analysed using the 'CANOPY' package (Ecosystem Dynamics, Research School of Biological Sciences, Australian National University). CANOPY determined the proportion of canopy gap for each of five zenith angle classes, representing equal projected portions of the sky (sAnderson 1964), with mid-points at θ_i=17.0°, 30.4°, 40.8°, 52.2°, and 69.5°. A frequency histogram of pixel intensity was produced for each photograph to determine the threshold between sky and foliage (Harper 1987). In all cases, the frequency histogram was bimodal, with peaks corresponding to sky and foliage image attributes. The trough between the peaks was used to determine a threshold value (Fig. 3.3) for allocating pixels to either sky or foliage classes, as used by Harper (1987). The "inversion technique" of Norman and Campbell (1989), outlined above, was used to calculate total plant area index from the gap fraction data for each zenith angle class in each photograph.

Tree characteristics on rainforest and eucalypt plots.

(a) Species selection, dbh and biomass.

Within each 30 x 30 m plot, eight trees were selected with trunk diameter at breast height (dbh) > 15 cm. On rainforest plots *Ceratopetalum apetalum* and *Doryphora*

sassafras were the dominant tree species, and four trees of each species were chosen on each plot (Table 3.2). On eucalypt forest plots, the overstorey vegetation was virtually a monospecific stand of *Eucalyptus maculata*. Consequently, eight trees of this species were chosen on these plots (Table 3.2). The dbh was estimated from measurement of the circumference of each tree. In all cases trunks were approximately circular in cross-section.

Above ground biomass (kg) for eucalypt (W_e) and rainforest (W_r) trees was calculated from published regression equations by Ash and Helman (1990). These equations were derived from measurements of dbh (cm) and tree mass from 67 rainforest and 66 eucalypt forest trees in a catchment of similar floristic composition situated 5 km from the field site. Tree biomass of *E. maculata* was calculated as,

$$\log_{10} W_e = -0.72 + 2.43 \log_{10} \text{dbh} \qquad (3.7)$$

and for rainforest species,

$$\log_{10} W_r = -0.63 + 2.34 \log_{10} \text{dbh} \qquad (3.8)$$

(b) Sapwood area.

The radial width of sapwood conducting tissue was determined by taking 4 mm diameter increment cores from each tree at two points on opposite sides of the trunk. In *E. maculata,* the sapwood associated with unblocked xylem vessels, was readily determined by the transmission of a bright light source through vessels. Open vessels were observed as points of light with the naked eye. In the two rainforest species, vessels were narrower and this technique could not be used. Instead, sapwood width was determined by injecting 5.5 ml 0.1% Schiff's reagent (acidified basic fuschin) into two 4 mm diameter holes, 80 mm deep, on opposite sides of the tree. Twenty-four

hours later a 4 mm wood core was removed 30 mm above each dye injection. The zone of stained conducting tissue was visible where the sap stream had transported the reagent. Comparison of both techniques in cut saplings of *E. maculata* (Chapter 4) showed that the stained tissue corresponded to unblocked vessels. Therefore, the stained region was considered equivalent to conducting tissue in both rainforest and eucalypt species. Sapwood area, A_S, was calculated,

$$A_S = \pi (r_o^2 - r_i^2) \qquad (3.9)$$

where r_o and r_i are the outer and inner radial boundaries of sapwood, respectively.

(c) Crown area.

The crown area of each tree was estimated from the vertical projection of the canopy boundary onto the ground (Table 2). Crown area, A_C, was estimated from the average circular area derived from three measurements of canopy diameter, *d*, separated by 60° each (Fig. 3.3) ,

$$A_C = \frac{\pi (d_1^2 + d_2^2 + d_3^2)}{12} \qquad (3.10)$$

This measure of crown area, on sloping sites, may be greater than the equivalent projection onto a horizontal surface. The maximum differences between any single canopy diameter, measured along the ground surface, and the equivalent diameter on the horizontal was 12% on the sheltered aspect rainforest plot (ie. 1 - Cosine 28.8°, Table 3.1). On other plots the maximum difference was less than 2%. Consequently, crown area is only slightly greater than the horizontal area occupied by the canopy of each tree. However, crown area ignores foliage distribution and any gaps within the canopy itself (Specht 1981, 1983).

Analysis of variance, computed in Genstat-5 (Lane *et al.* 1987; Digby *et al.* 1989), was used to compare tree measurements between plots. Since there was no effective replication of plots, the analysis of variance was based upon within plot to between plot variance. Extrapolation of results to other locations requires the assumption that plot choice was random within the forest. This assumption remains untested. However, plots appeared representative of the forest on a given aspect. Thus, it was considered that conclusions based on the anova, may be extrapolated to the whole forest.

Results

Distribution of rainforest and eucalypt forest vegetation.

Vegetation within the study site was distributed differentially with aspect (Fig. 3.1). Rainforest was largely confined to sheltered aspects, to within 60 m of the ridge top, and along both tributaries of the water course. On exposed aspects, rainforest vegetation was confined to within 40 m upslope of the water course, with a band of ecotonal vegetation up to 80 m wide, further upslope. Ecotonal vegetation also occurred upslope of rainforest on the sheltered slope. Within the ecotone and rainforest vegetation on the sheltered aspect, were several large eucalypts overtopping rainforest suggesting a recent upslope shift in the rainforest boundary. On the exposed aspect, however, no evidence of boundary movement was present.

Plant area index.

(a) Application of the hemispherical photographic technique.

Plant area index is a measure of leaf, branch and stem area of the canopy. Estimated plant area index from digitised hemispherical canopy photographs was dependant on the threshold value chosen to distinguish between foliage and sky (Fig. 3.5). With increasing threshold, lighter tones were partitioned to foliage in the digitised image. It was noted that as threshold increased, pixels were partitioned to foliage beginning at the edge of large gaps and proceeding to the centre. Thus, as the threshold increased, gap size decreased. Arbitrary estimation of the threshold value may lead to erroneous estimation of the gap frequency. A single threshold value was determined for each photograph in the present work, by plotting the pixel frequency as a function of pixel intensity (Fig. 3.3), and locating the minimum pixel frequency between sky and foliage image attributes. Threshold values ranged from 127 to 148, for all photographs. Thus, the frequency histogram of pixel intensity (Fig. 3.3) provided an objective means for calculating the threshold value (Harper 1987). Printing and digitising procedures were kept constant between photographs. Therefore, variation in the threshold value betwen photographs may be due to variation in the image density between negatives.

The effect of variation in camera exposure on plant area index, with threshold kept constant (Fig. 3.6), was similar to that of increasing the threshold value and maintaining photographic exposure constant (Fig. 3.4). However, this effect was more pronounced in eucalypt than in rainforest canopy photographs (Fig. 3.6). The variation in plant area index with exposure was partly due to the relationship between light and gap geometry. Again, pixels at the edges of gaps were progressively partitioned from sky to foliage as exposure decreased, thereby reducing gap size in the digitised image. However, inspection of the pixel frequency histograms of these photographs indicated another cause (Fig. 3.7a and 3.7b). As photographic exposure decreased from +1 to 0, the

frequency of pixels corresponding to foliage increased (Fig. 3.7a) and those corresponding to sky decreased (Fig. 3.7b). Further decrease in exposure by 1-stop, resulted in a shift in the histogram to the left, and a further reduction in pixel frequency corresponding to the sky (Fig. 3.7b). Inspection of the canopy photographs at different exposures indicated that the reduction in pixel frequency corresponding to sky was due to the high reflectivity and the steep inclination of eucalypt leaves. At 1-stop overexposure, steeply inclined eucalypt leaves at low zenith angles (ie. overhead), were indistinguishable from the sky. In rainforest canopy photographs (Fig 3.7c and 3.7d) the effect of reducing photographic exposure from +1 to 0 stops was less pronounced, presumably because of lower reflectivity and lower leaf inclination angles. However, at -1 stop, a reduction in pixel frequency corresponding to sky was observed.

Canopy photographs at the metered exposure were preferred for measurements of gap fraction using the inversion technique because they displayed the most even sky tone, maximum contrast between sky and foliage, particularly in eucalypt canopy photographs, and minimum flaring of sky light at the edges of gaps. As an independent check of this choice of exposure, foliage area (ignoring stem and branch area) per tree was compared with unpublished equations from Ash and Southern (1982) of leaf area per tree as a function of dbh in a nearby catchment containing *E. maculata* forest and rainforest (Fig. 3.8). Ash and Southern (1982) measured leaf area on six 2 cm diameter branches of rainforest and eucalypt forest trees, then counted the number of 2 cm branches on 78 trees over a wide range of dbh to estimate total leaf area per tree. In the present study, mean canopy foliage area per tree (FA) was derived from mean values of plant area index (PAI), and crown area (A_C),

$$FA = PAI \times A_C \qquad (3.11)$$

Estimates of foliage area using equation 3.11 were within 8% and 43% of the estimates of leaf area using the regression equations (Ash and Southern 1982) for sheltered and

exposed aspect eucalypt forest plots, and within 5% and 23% of the regression equations for the gully bottom and sheltered aspect rainforest plots, respectively.

(b) Plant area index on rainforest and eucalypt forest plots.

Analysis of variance showed significant differences in plant area index between plots and seasons (Table 3.3, Fig. 3.9). Mean plant area index was significantly higher in the rainforest canopy, than in the eucalypt canopy at all times of the year. Additionally, mean plant area index was higher in the exposed aspect eucalypt forest in summer, compared to winter or autumn ($p < 0.05$), and was lower in both sheltered aspect plots in autumn than in summer ($p < 0.05$). Plant area index in the gully bottom rainforest plot was higher in summer and autumn than in winter ($p < 0.05$).

Tree characteristics on rainforest and eucalypt plots.

Analysis of variance on measurements of dbh, crown area, sapwood area and biomass was used to compare between rainforest and eucalypt field plots (Fig. 3.10). Inspection of residuals for each analysis indicated homogeneity of variance between plots. None of the measured parameters differed between *D. sassafras* and *C. apetalum*. Hence data for both species were pooled and comparisons were made between rainforest and eucalypt forest.

Eucalypt forest plots had significantly greater mean dbh, crown area and tree biomass than rainforest plots ($p < 0.05$, Fig. 3.10). However, within each forest type, variation between plots was not significant. Mean sapwood area per tree was not significantly different between rainforest and eucalypt forest. This was due to a wider sapwood width in rainforest trees for a given dbh, than in eucalypt trees.

The relationship between ln(crown area) and ln(dbh) was not different between rainforest and eucalypt trees (Fig. 3.11a), even though eucalypts tended to have a greater mean dbh and mean crown area than rainforest trees (Fig. 3.10). The relationship between ln(biomass) and ln(crown area), however, differed between rainforest and eucalypt trees (Fig. 3.11b). For a given biomass, the crown area in rainforest trees tended to be larger than in eucalypts, although mean biomass and mean crown area in eucalypts was greater than in rainforest trees (Fig. 3.10). Additionally, there were no differences between plots within each forest type. Mean plant area index per plot over all seasons, was linearly related to the ratio of sapwood area per unit crown area on each plot (Fig. 3.12). Thus, higher plant area index on the rainforest gully bottom plot, was correlated with more sapwood area per unit crown area.

Discussion

Distribution of rainforest and eucalypt forest vegetation.

Exposed north facing aspects may receive high ground surface irradiance resulting in higher soil and air temperatures and lower soil moisture and humidity (Hutchins *et al.* 1976; Tajchman and Lacey 1986; Tajchman *et al.* 1988; Feldhake and Boyer 1990). As a consequence, variation in both vegetation biomass and species diversity with aspect has been observed both in forest sites (Cantlon 1953; Lundqvist 1968; Mowbray and Oosting 1968; Day and Monk 1974; Hutchins *et al.* 1976; Tajchman and Lacey 1986; Lipscomb and Nilsen 1990a and 1990b; Hairston and Grigal 1991) and pastures (Ludwig *et al.* 1957; Pigott 1968; Pope and Lloyd 1975; Radcliffe 1982). Rainforest and eucalypt forests in eastern temperate Australia, are also differentially distributed with variation in aspect (McLuckie and Petrie 1927; Fraser and Vickery 1938; Burges and Johnston 1953; Baur 1957; Florence 1964; Turner 1976; Yates 1989). At the study

site, rainforest was located along the gully base and on sheltered aspects whereas eucalypt forest occurred on exposed aspects and ridge tops (Fig. 3.1). Rainforest occurred up to 40 m upslope of the water course on the exposed aspect. However, rainforest extended up to 300 m upslope above the water course, to within 60 meters of the ridge top on the sheltered aspect. The ecotonal vegetation on exposed aspects, extended up to 80 meters upslope from the rainforest. In other locations in southeastern New South Wales, ecotone vegetation was confined to within a few meters of the rainforest edge on northern aspects particularly at high slope angle (Yates 1989) whereas on sheltered aspects, ecotonal vegetation extended between 5 and 60 m upslope of rainforest vegetation.

Several large eucalypts were present within the rainforest boundary on the sheltered apsect, but not on the exposed aspect at the field site. Eucalypt seedlings do not regenerate beneath a closed canopy (Ashton 1981). Thus, large individual eucalypt trees within the rainforest boundary, must have established prior to upslope migration of rainforest. Allometric relationships betwen growth ring number and dbh (Ash and Helman 1990), indicate that establishment of these eucalypt trees may have occurred more than 150 years ago. Similar patterns of migration by rainforest into eucalypt forest, have been observed throughout eastern Australia (Cremer 1960; Turner 1976; Unwin *et al.* 1985; Ash 1988; Unwin 1989a and 1989b), and may be controlled by interactions between present day climate and fire regimes, but mediated by edaphic and topographic factors (Ash 1988; Unwin 1989a).

Plant area index.

(a) Application of the hemispherical photographic technique.

Plant area index is a measure of stem, branch and leaf area index of the canopy. The hemispherical photographic technique may be used to estimate plant area index in forest canopies (Norman and Campbell 1989), however, results may be biased by any of the processes used to convert the canopy image to gap fraction data (Fig. 3.13). Both the printing and digitising procedures were kept constant in the present work, consequently sources of bias were restricted to photographic exposure and the threshold value. Bias due to incorrect threshold values is caused by the variation in gap brightness due to gap geometry (Fig. 3.5). Pixel intensities near gap edges have lower intensity than near the centre, presumably due to both averaging of foliage and sky in each pixel and to penumbral effects of the canopy gap. Thus, a reduction in threshold resulted in partitioning of pixels from sky to foliage firstly at the edges of gaps, thereby decreasing gap fraction and increasing plant area index. The bias due to incorrect threshold, however, is eliminated by determination of the threshold value for each image independently.

Variation in photographic exposure may have two effects on image intensity (Fig. 3.14). Firstly, the intensity of the whole image may change, but the relative difference between sky and foliage may remain the same (Fig 3.14a). Secondly, photographic exposure may alter the proportion of sky and foliage recorded on the film (Fig. 3.14b). The first effect may be compensated for by adjusting the threshold value (T_1 to T_2 in Fig. 3.14a). The second effect, however, cannot be compensated for during the digitising procedure because the bias is recorded on the negative. Inspection of images and frequency histograms (Fig. 3.7), indicated that bias associated with the second effect was due to fogging of light around the edges of leaves and stems at low zenith angles. Thus, the reduction in plant area index with increasing exposure, at a constant

threshold value (Fig. 3.6), was due to (a) flaring of light around steeply inclined eucalypt leaves, (b) high leaf reflectivity, and (c) variation in overall intensity of the whole image. Chen *et al.* (1991) reported a similar decrease in plant area index with increasing exposure in *Pseudotsuga menziesii* forest, due to flaring of light around leaves at higher exposures.

The criteria used to determine photographic exposure varies between published reports. Anderson (1981) and Harper (1987) used a range of exposures then selected photographs on the basis of visual inspection of the image. Rich (1989) used the camera metering system to determine photographic exposure, and then suggested that greatest clarity was acheived by photographing the canopy at 1-stop underexposure. Once photographs have been digitised, Rich (1989) suggested that the threshold value may be adjusted until a "best match" is obtained between image and photograph. Chen *et al.* (1991) suggested that a 1- to 2-stop underexposure, measured under overcast skies outside the canopy, gave values of plant area index comparable to the Li-Cor Plant Canopy Analyser for *P. menziesii* forest. However, the criteria by which sky and foliage image attributes were partitioned were not presented in their study. The thresholding technique is superior to using "best match" techniques for partitioning pixels to foliage and sky image attributes because it removes any bias associated with estimation of the threshold value. However, thresholding will not compensate for errors introduced by photographic exposure. Clearly there is a need for calibration of the technique if absolute measurements of plant area index are to be made.

A single pixel in the digitised image of a hemispherical canopy photograph at zero zenith angle (ie. overhead), when projected to the height of the forest canopy at 20 to 30 m, represents a square of sides approximately 12 to 19 cm, respectively. The area encompassed by this pixel will be greater than the size of a single leaf in either rainforest or eucalypt forest. Consequently, the pixel intensity produced by the digitiser will represent the average intensity of the sky and foliage for that pixel. The frequency

histogram of pixel intensity for canopy photographs (Fig. 3.3 and 3.7) indicated that most pixels cluster as either foliage or sky image attributes. Pixels falling between these two peaks correspond to those at the edges of foliage or foliage clumps (Harper 1987). The threshold value assigns these middle intensity pixels to either "mostly" sky or "mostly" foliage, leading to the possibility that some error may be associated with pixel categorisation. However, because the majority of pixels fall into either sky or foliage attributes, the histogram peak corresponding to sky is a measure of the gap fraction which itself is a function of the plant area index of the canopy (equation 3.3).

(b) Canopy leaf area index.

In order to determine leaf area index from measures of plant area index, an estimate of the stem and branch area (the woody area index, WAI, Chason *et al.* 1991) must be obtained. In deciduous forest measurement of WAI may be easily acheived by re-photographing the canopy after autumn leaf fall. However, estimates of WAI in evergreen forest must be made by direct measurements. Woody area index has been estimated at 9.8% (PAI = 5.1, Neumann *et al.* 1989) and 12% (PAI = 4.89, Chason *et al.* 1991) of the plant area index in oak-hickory forest and comprised 6.6% of the "total surface area index" in a *Pinus radiata* canopy (Lang *et al.* 1991). We may expect a similar value for the WAI of about 10% plant area index in the present work. Thus, plant area index in rainforest and eucalypt forest canopies is composed mostly of the leaf area index component. The WAI remains virtually constant throughout the year, therefore changes in plant area index (Fig. 3.9) are probably due to variation in leaf area index between seasons. This suggestion is supported by observed seasonal shoot growth between September and November in *E. maculata* forest (Pook 1984a). Seasonal variation in leaf area index has also been observed in coniferous forest (Beadle *et al.* 1982; Gholz *et al.* 1991).

Photographic exposures using the camera's automatic metering system were judged as most suitable considering the separation of sky and foliage tones, flaring of light in gaps and clarity of image. This choice was supported by independent estimation of leaf area by Ash and Southern (1982) in rainforest and eucalypt forest near the field site. Additionally, estimated plant area indices in the present work are similar to published reports. Harper (1987) estimated plant area indices using hemispherical photographs, of between 3.07 and 4.52 for temperate rainforest of similar species composition to the present work, near Wollongong, New South Wales. Mean values in the present study for both rainforest plots, pooled over all seasons, was 3.79. Anderson (1981), using hemispherical photographs and direct measurements, and Pook (1984b), using direct methods, measured leaf area indices of between 1.1 and 1.96, and between 2.65 and 3.12, respectively, in *E. maculata* overstorey in the Kioloa State Forest. Mean values of plant area index in the present study for *E. maculata* forest, pooled over all seasons was 2.55. Carbon *et al.* (1979a), using visual estimation of leaf area index against photographic standards, reported values of leaf area indices between 1.4 and 2.1 for *Eucalyptus marginata - Eucalyptus calophylla* forests, 1.3 for mature *Eucalyptus diversicolor* forests in southwestern Western Australia, and 1.9 for *E. regnans* forest in Victoria (Carbon *et al.* 1979b).

(c) Foliage inclination angle.

The mathematical "inversion technique" estimates plant area index (equation 3.4) as the sum of L_j for all leaf inclination classes (Norman and Campbell 1989). The relative proportion of plant area index in each foliage inclination class may be obtained from the ratio $L_j:L_o$. This ratio represents the proportion of plant area index with normals in the solid angle represented by the mid-point of that inclination class. Figure 3.15 shows the mean proportion of plant area index in each inclination class for five photographs, on each plot at the field site. In eucalypt forest, on both exposed and sheltered plots, a higher proportion of foliage area index was observed in higher inclination classes in all

seasons, except for winter measurements on the exposed aspect (Fig 3.15a). Inspection of canopy photographs showed no obvious reason for the opposite trend in foliage inclination in winter. In both rainforest sites, however, the proportion of foliage area index tended to be more evenly distributed between leaf inclination classes, except for the gully bottom site which displayed an extremophile distribution in summer (Fig. 3.15b). That is, foliage was predominantly distributed in either horizontal or vertical inclinations (Ross 1981). Determination of leaf angle distribution from inversion techniques has been reported for *Pseudotsuga menziesii* forest (Chen *et al.* 1991) but criticised as being inaccurate by Lang *et al.* (1985) and Chen and Black (1991), since gap fraction measurements contain information on both foliage element inclination and foliage clump, stem and branch geometry. Miller (1967) showed from direct measurements, that leaf inclination angle was a function of height in the canopy in *Quercus gambellii* and *Populus tremuloides* forest. Horizontal leaves occurred more frequently lower in the canopy, whereas leaves at the top of the canopy had higher leaf inclination angles. In some cases, the porportion of plant area index in each inclination class supported the hypothesis that the *E. maculata* canopy had higher leaf inclination angles than rainforest. However, the presence of anomalous results, such as the reversal of the trend in Fig 3.15a, indicates potential errors in estimating foliage inclination using the hemispherical technique.

Tree characteristics on rainforest and eucalypt forest plots.

Whereas rainforest and eucalypt forest distribution was related to aspect (Fig. 3.1), tree diameter at breast height (dbh), crown area and biomass per tree within each forest type were not (Fig. 3.10). Differences between vegetation types are summarized for each plot in Fig. 3.16. Eucalypt forest trees had greater dbh, crown area and biomass than rainforest trees. The allometric relationship between crown area and dbh (Fig. 3.11a) was similar between rainforest and eucalypt forest. This relationship may indicate an

underlying mechanical requirement for a given trunk diameter necessary to maintain stability for a given crown area, irrespective of species differences. Relationships between trunk diameter and tree height in temperate and tropical tree species of North and Central America, are considered to represent convergent strategies which facilitate both height growth, in order to maximise net energy interception, and prevent buckling of the trunk under load (King 1990a, 1990b and 1991b). The relationship between biomass and crown area, however, was different between forest types (Fig. 3.11b). The crown area per unit biomass was higher in rainforest trees than in eucalypts, even though mean biomass and mean crown area were higher in eucalypts (Fig. 3.10). High leaf area index, more horizontal leaf orientation and a wider crown per unit biomass in rainforest trees may increase light interception and reduce understorey irradiance, thereby shading more light demanding species. Thus, a wider crown per unit biomass may be advantageous under light limiting conditions, such as occurs on sheltered aspects during winter. However, greater canopy interception may be deleterious under high irradiance if it contributes to a greater evaporative demand. A less extensive canopy area per unit biomass in eucalypt trees, lower leaf area index and greater leaf inclination angle may avoid interception of high radiation on exposed aspects. These features may be advantageous in locations of low water availability.

Allometric relationships have been observed between sapwood area and canopy leaf area in many tree species (Shinozaki *et al.* 1964; Waring *et al.* 1977; Whitehead and Jarvis 1981; Waring 1983; Zimmermann 1983; Marshall and Waring 1986;). Thus, as the potential evaporating surface of the canopy increases, there is a concomitant increase in conducting tissue, presumably to maintain water supply to leaves. In the present study, mean sapwood area was similar between forest types and between plots. However, sapwood area per unit crown area was linearly related to mean plant area index, estimated from canopy photographs (Fig. 3.12). This suggests a functional relationship between canopy leaf area and sapwood area (Whitehead 1985 and 1988). Higher leaf area, and the associated higher evaporative demand, may be supported on

more mesic sites, such as the gully bottom, by greater water availability. This suggestion is consistent with other studies on the relationship between leaf area and site water availability at larger spatial scales (eg. Grier and Running 1977; Gholz 1982).

Influence of aspect on rainforest and eucalypt forest distribution.

Vegetation distribution patterns in the present study, agree with those reported for this region by Yates (1989) and with distribution patterns of rainforest and eucalypt vegetation in northern New South Wales and southern Queensland (McLuckie and Petrie 1927; Fraser and Vickery 1938; Baur 1957; Florence 1964; Turner 1976; Burges and Johnston 1953). Canopy structure may have a profound influence on energy balance, transpiration and understorey micreonvironment (Campbell and Norman 1989). Thus, differences in canopy structure between rainforest and eucalypt forest species may have adaptive advantages on natural light and water gradients in southeastern New South Wales. The second hypothesis from Chapter 1 proposed that rainforest canopies would have higher leaf area indices and lower leaf inclination angles than euclaypt forest, and that these differences in canopy structure may be related to differences in transpiration from each forest type. Different water use strategies between species may indicate processes which contribute to the differential distribution of vegetation types with aspect. This chapter has quantified differences in canopy structure between forest types, and chapter 5 investigates differences in water use characteristics.

Measurements of plant area index using the hemispherical photographic technique support the hypothesis that leaf area index is higher in rainforest than eucalypt forest. Plant area index increased in both forest types in summer and decreased by autumn, presumably due to seasonal leaf growth and leaf fall, respectively. Tree size characterisitics on forest plots also varied between vegetation types but not between

plots. Larger crown area per unit biomass in rainforest trees may increase light interception per tree at high leaf area indices which may be advantageous on sheltered aspects. However, greater leaf area, crown area per unit biomass and apparently more horizontally orientated leaves in rainforest species, may increase the evaporative demand for water under high irradiance. Thus, rainforest canopy species may be disadvantaged compared with eucalypts, under conditions of high irradiance and low soil moisture, such as exposed aspects and ridgetops. Lower leaf area indices and apparently more steeply inclined leaves in eucalypts may be advantageous in drier environments. Thus, inherent differences in canopy structure between foliage types, may contribute to determining the differential distribution of vegetation types in eastern temperate Australia.

Table 3.1.
Characteristics of four 30 x 30 m plots located within rainforest and eucalypt forest at the field site in the Kioloa State Forest, New South Wales.

Forest type	Mean slope angle	Aspect
Sheltered aspect eucalypt forest	9.6°	185°
Sheltered aspect rainforest	28.8°	214°
Gully bottom rainforest	7.4°	340°
Exposed aspect eucalypt forest	12.0°	341°

Table 3.2.

Summary information for eight trees on each of four plots at the field site in the Kioloa State Forest, New South Wales. dbh, diameter at breast height (cm), Sapwood area (cm^2) and A_c, crown area (m^2).

Tree No.	Species	Plot	dbh	Sap wood area	A_c
1	*C. apetalum*	Sheltered aspect rainforest	26.3	338.9	17.6
2	*C. apetalum*	Sheltered aspect rainforest	18.6	194.7	12.4
3	*C. apetalum*	Sheltered aspect rainforest	43.1	600.8	80.0
4	*C. apetalum*	Sheltered aspect rainforest	29.0	289.4	39.2
5	*E. maculata*	Sheltered aspect eucalypt forest	67.0	428.5	120.4
6	*E. maculata*	Sheltered aspect eucalypt forest	35.0	182.2	45.9
7	*E. maculata*	Sheltered aspect eucalypt forest	53.8	366.8	106.4
8	*E. maculata*	Sheltered aspect eucalypt forest	60.7	392.4	117.5
9	*D.sassafras*	Sheltered aspect rainforest	46.1	1466.4	70.8
10	*D.sassafras*	Sheltered aspect rainforest	54.8	910.1	73.8
11	*D.sassafras*	Sheltered aspect rainforest	27.2	216.8	30.8
12	*D.sassafras*	Sheltered aspect rainforest	41.3	375.2	33.6
13	*E. maculata*	Sheltered aspect eucalypt forest	36.1	279.0	42.7
14	*E. maculata*	Sheltered aspect eucalypt forest	46.6	430.1	59.2
15	*E. maculata*	Sheltered aspect ecalypt forest	40.4	346.4	28.7
16	*E. maculata*	Sheltered aspect eucalypt forest	65.7	602.4	97.5
17	*C. apetalum*	Gully bottom rainforest	21.5	205.3	13.0
18	*C. apetalum*	Gully bottom rainforest	35.1	361.4	14.1
19	*C. apetalum*	Gully bottom rainforest	29.5	603.8	20.35
20	*C. apetalum*	Gully bottom rainforest	51.2	666.3	70.9
21	*E. maculata*	Exposed aspect eucalypt forest	80.2	660.5	136.6
22	*E. maculata*	Exposed aspect eucalypt forest	59.2	463.7	68.4
23	*E. maculata*	Exposed aspect eucalypt forest	45.2	352.5	50.5
24	*E. maculata*	Exposed aspect eucalypt forest	36.8	241.1	57.9
25	*D.sassafras*	Gully bottom rainforest	24.2	208.4	15.3
26	*D.sassafras*	Gully bottom rainforest	37.1	593.7	13.2
27	*D.sassafras*	Gully bottom rainforest	42.2	670.3	44.6
28	*D.sassafras*	Gully bottom rainforest	25.1	344.7	29.8
29	*E. maculata*	Exposed aspect eucalypt forest	64.6	561.9	79.7
30	*E. maculata*	Exposed aspect eucalypt forest	67.7	623.1	82.2
31	*E. maculata*	Exposed aspect eucalypt forest	40.8	301.6	28.5
32	*E. maculata*	Exposed aspect eucalypt forest	91.5	532.8	233.4

Table 3.3.
Summary table for the analysis of variance showing degrees of freedom (d.f.), variance ratios and their significance for all plot, season and plot x season effects on plant area index estimated by hemispherical photography in four plots in the Kioloa State Forest, for winter and summer 1991, and autumn 1992. * significant $P < 0.05$; ** significant $P < 0.01$.

		Variance ratio
Source	d.f.	Plant area index
plot	3,42	58.83**
season	2,42	28.08**
plot x season	6,42	3.09*

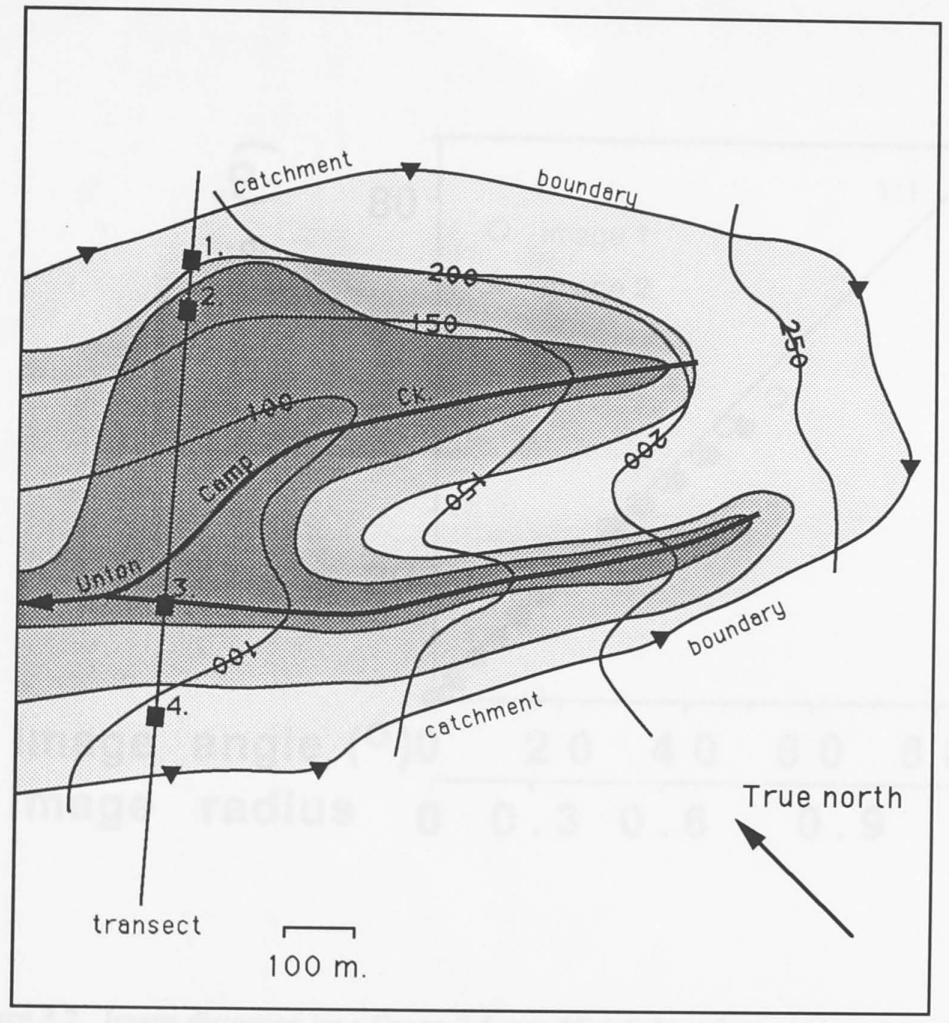


Figure 3.1. Vegetation distribution pattern at the field site in the Kioloa Flora Preserve, on Union Camp Creek, Kioloa State Forest, NewSouth Wales (35°35'S, 150°20'E). Four 30 x 30 m plots were positioned along a transect of 220°azimuth.

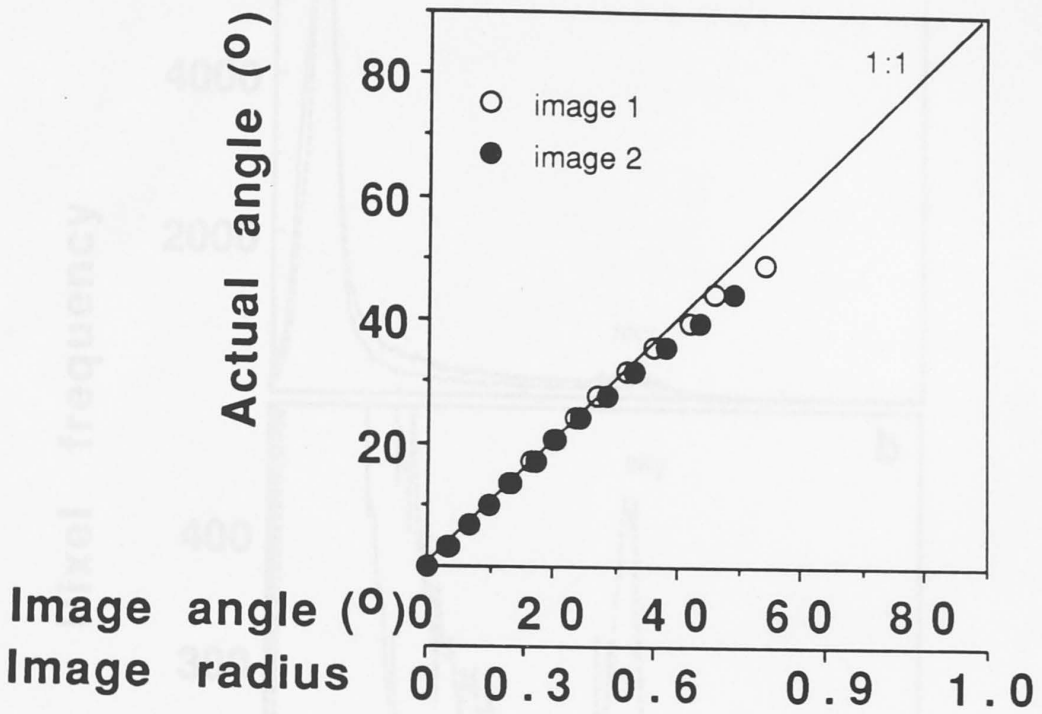


Figure 3.2. Image distortion by a Canon 7.5 mm f/5.6 fisheye lens used to photograph rainforest and eucalypt forest canopies. Actual angles were compared with those recorded at the film plane (the image angle).

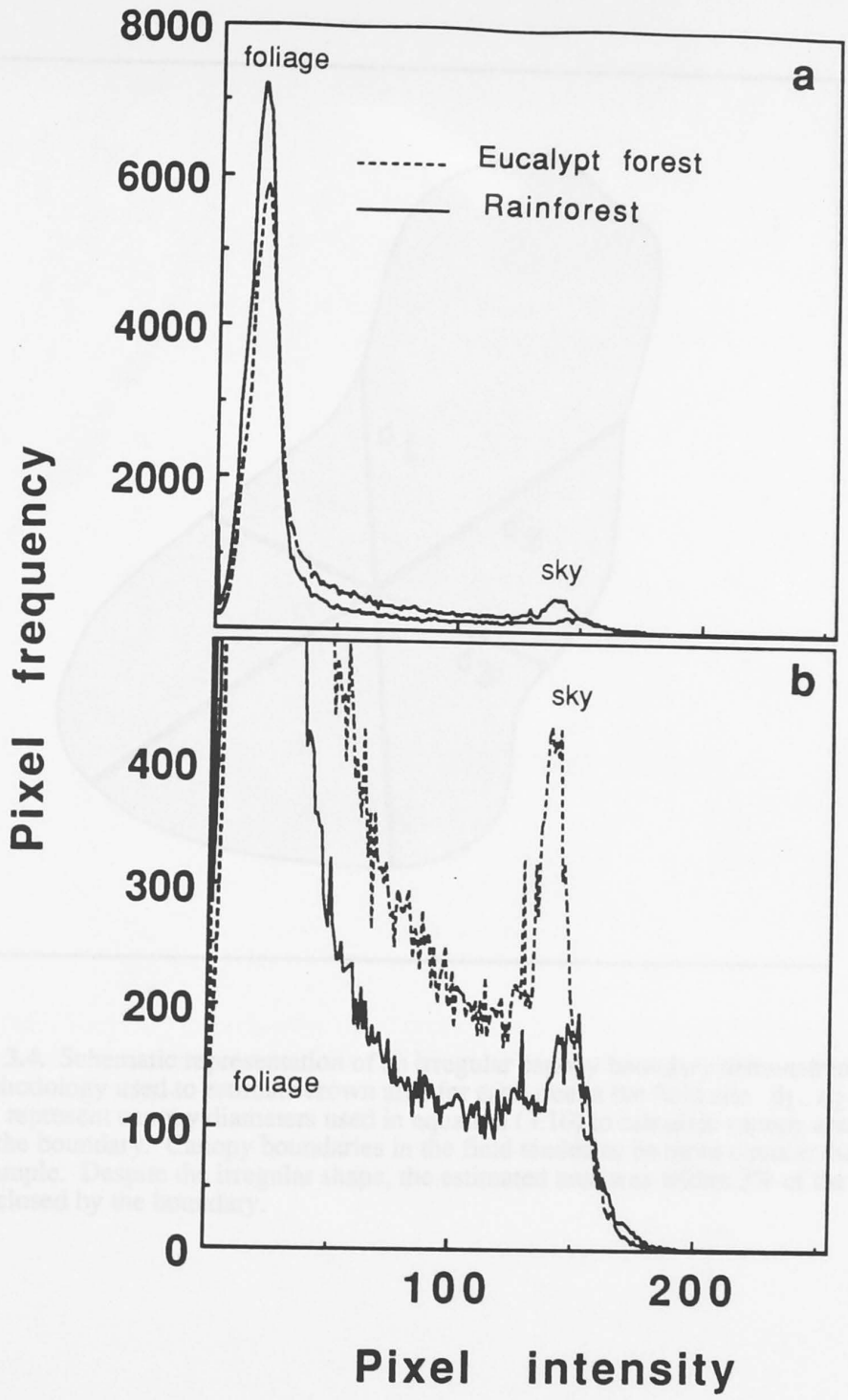


Figure 3.3. Histograms of pixel frequency as a function of pixel intensity, in digitised hemispherical photographs of the rainforest and eucalypt forest canopy on the exposed aspect plot, in autumn 1992. (a) Complete frequency histogram. (b) Expanded y-axis to show peak corresponding to the sky image attribute.

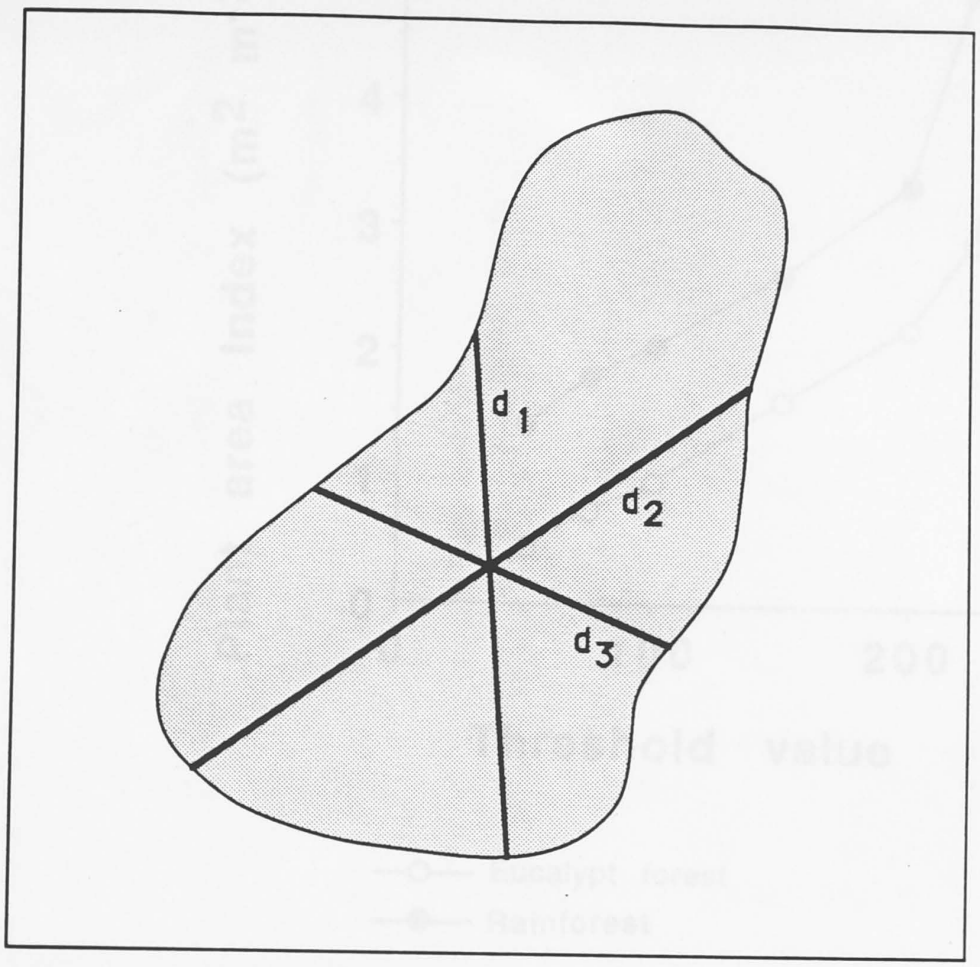


Figure 3.4. Schematic representation of an irregular canopy boundary demonstrating the methodology used to estimate crown area for each tree at the field site. d_1, d_2 and d_3 represent canopy diameters used in equation (3.10) to calculate canopy area within the boundary. Canopy boundaries in the field tended to be more circular than this example. Despite the irregular shape, the estimated area was within 3% of the area enclosed by the boundary.

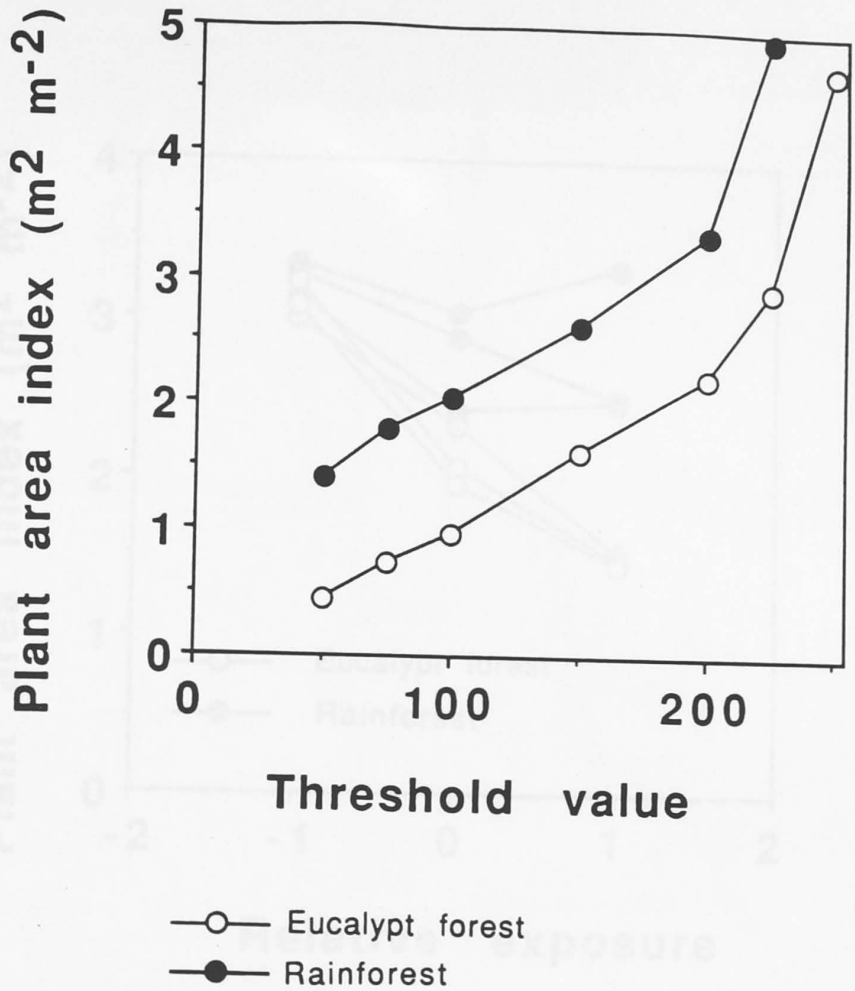


Figure 3.5. Variation in estimated plant area index as a function of threshold value. Data derived from images of rainforest and eucalypt forest canopies in the gully bottom and exposed aspect plots, respectively, in autumn 1992.

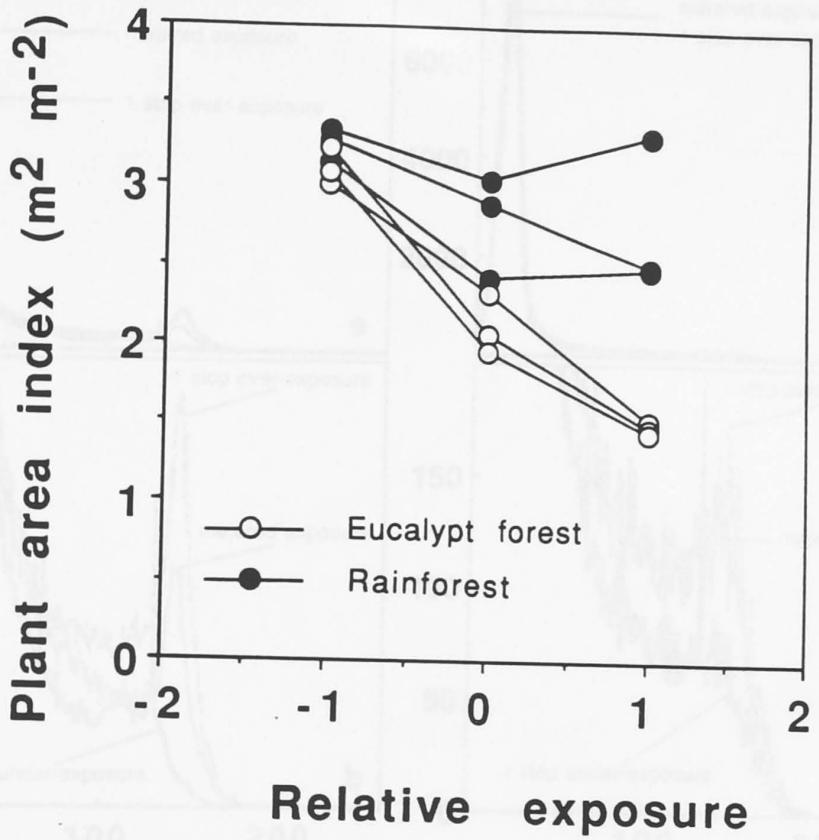


Figure 3.6. Variation in plant area index as a function of photographic exposure. Data derived from three hemispherical photographs of rainforest and eucalypt forest canopies, in the gully bottom and exposed aspect plots, respectively, in autumn 1992. A zero relative exposure represents that measured by the camera metering system at f/11 apeture. The threshold value was held constant at 143 and 140 for gully bottom and exposed aspect canopy photographs, respectively.

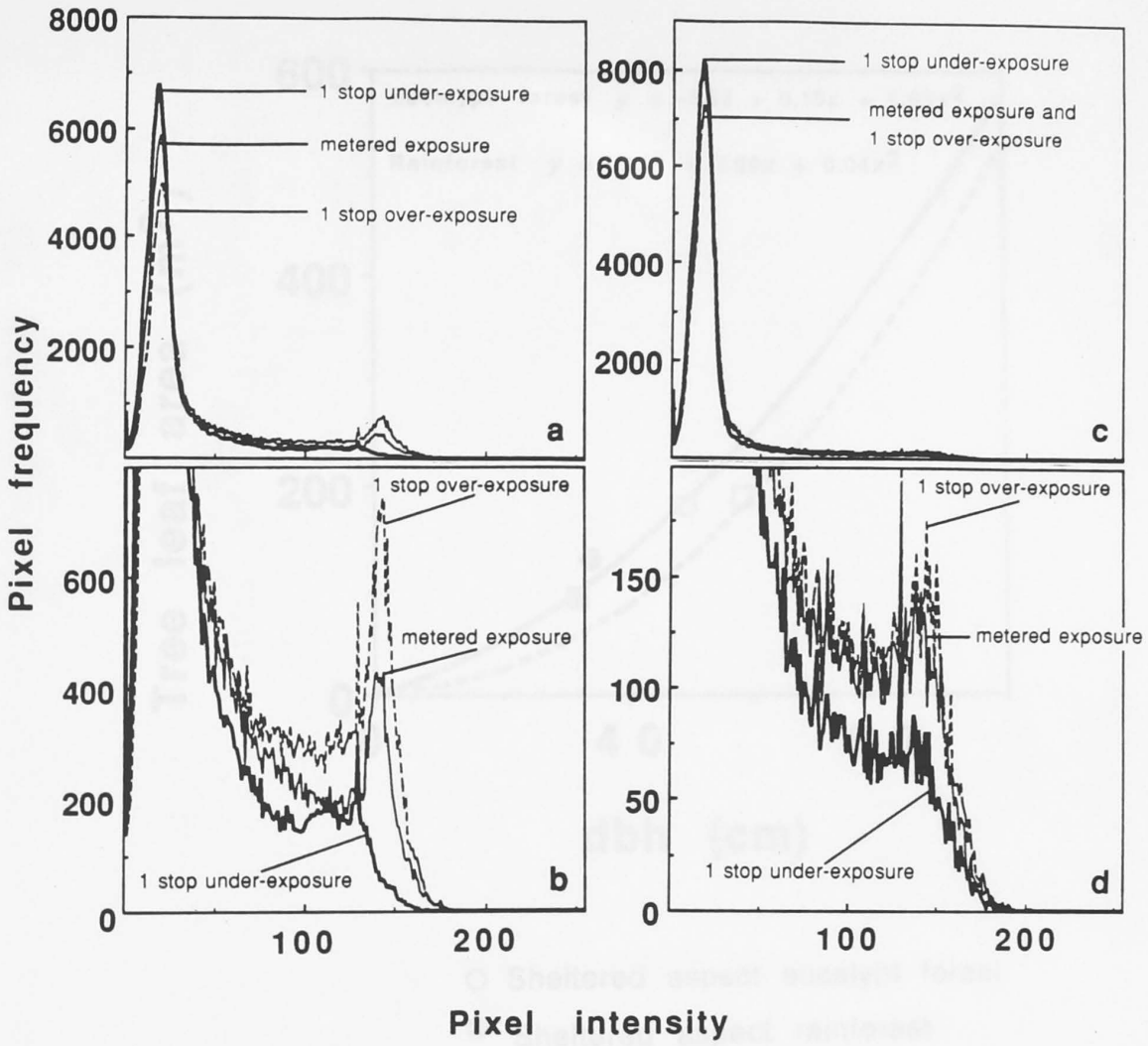


Figure 3.7. Effect of variation in photographic exposure on the pixel frequency histogram. Data derived from two photographs of eucalypt and rainforest canopies from the exposed aspect and gully bottom sites, respectively, in autumn 1992. (a) and (c) demonstrate the effect of photographic exposure on the whole freqency histogram, (b) and (d) have and expanded y-axis to enlarge the peak corresponding to the sky image attribute.

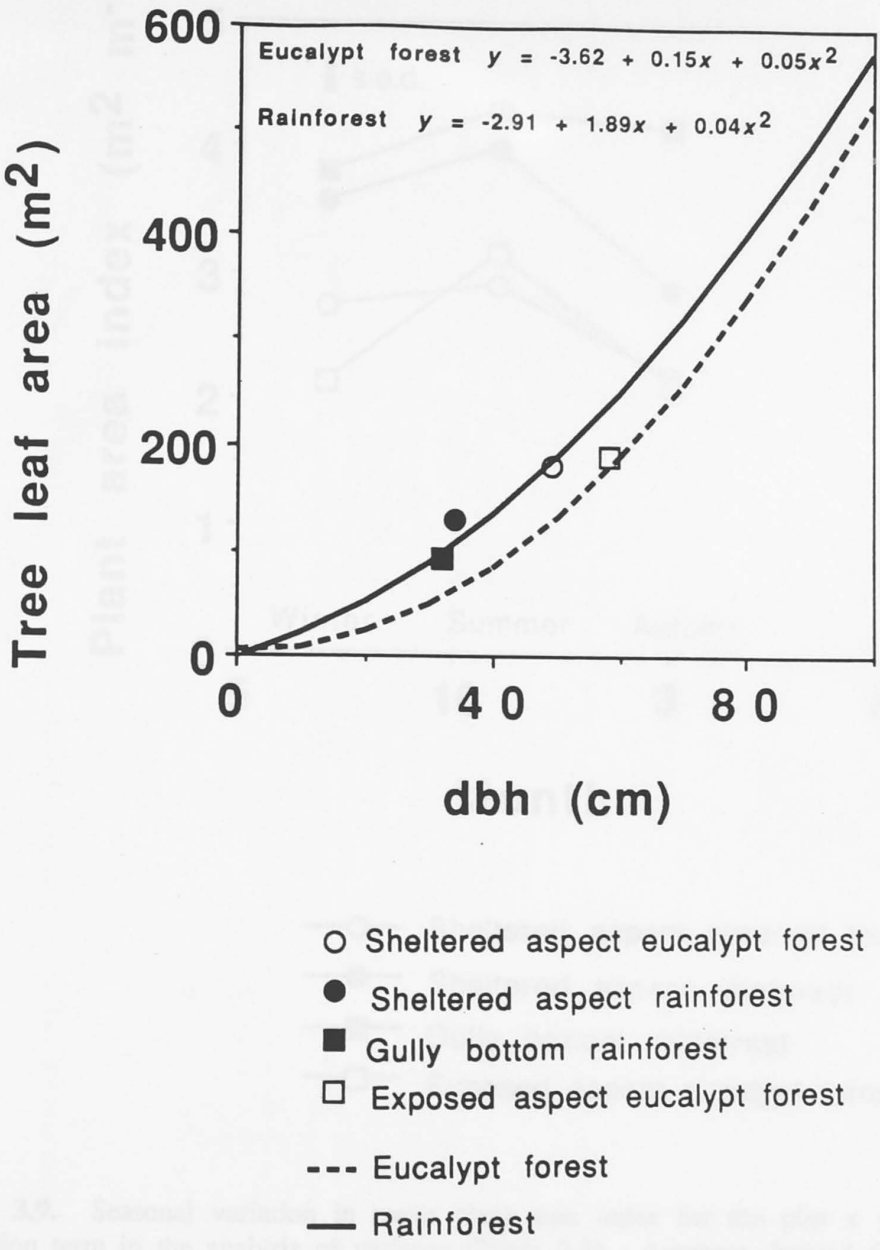


Figure 3.8. Mean tree leaf area in each plot as a function of mean tree diameter at breast height (dbh) in both rainforest and eucalypt forest plots at the field site. Data derived from mean crown area (Fig. 3.10) and mean plant area index (Fig. 3.9). See text for details of calculations. Curves plotted from relationships derived by Ash and Southern (1982, unpublished data).

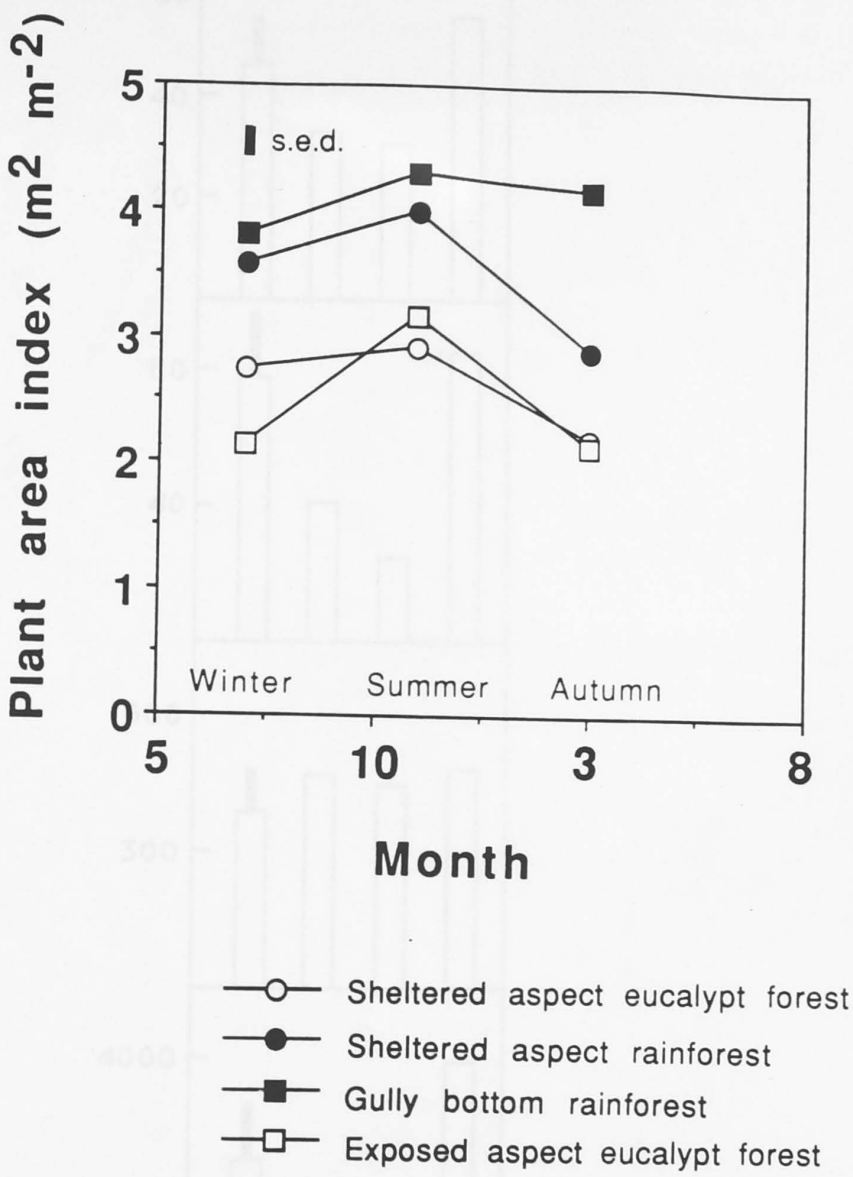


Figure 3.9. Seasonal variation in mean plant area index for the plot x season interaction term in the analysis of variance (Table 3.3). Averages derived from 5 photographs per plot for each season, except for both sheltered aspect plots during winter, when 2 photographs per plot were used. Vertical bar represents the standard error of the difference of means.

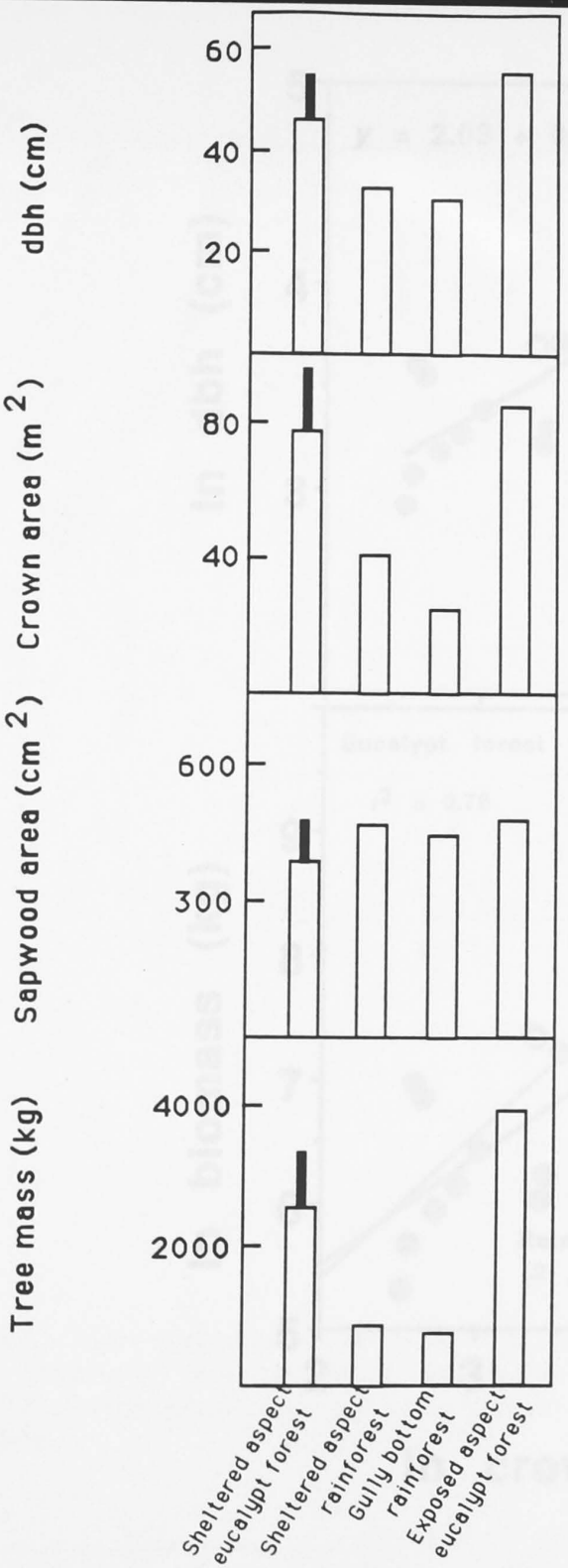


Figure 3.10. Mean tree diameter at breast height (dbh), crown area, sapwood area and tree biomass for four experimental plots in the Kioloa Flora Preserve. Means based on measurements of eight trees per plot, derived from an analysis of variance comparing plots. Vertical bars represent the standard error of the difference of the means.

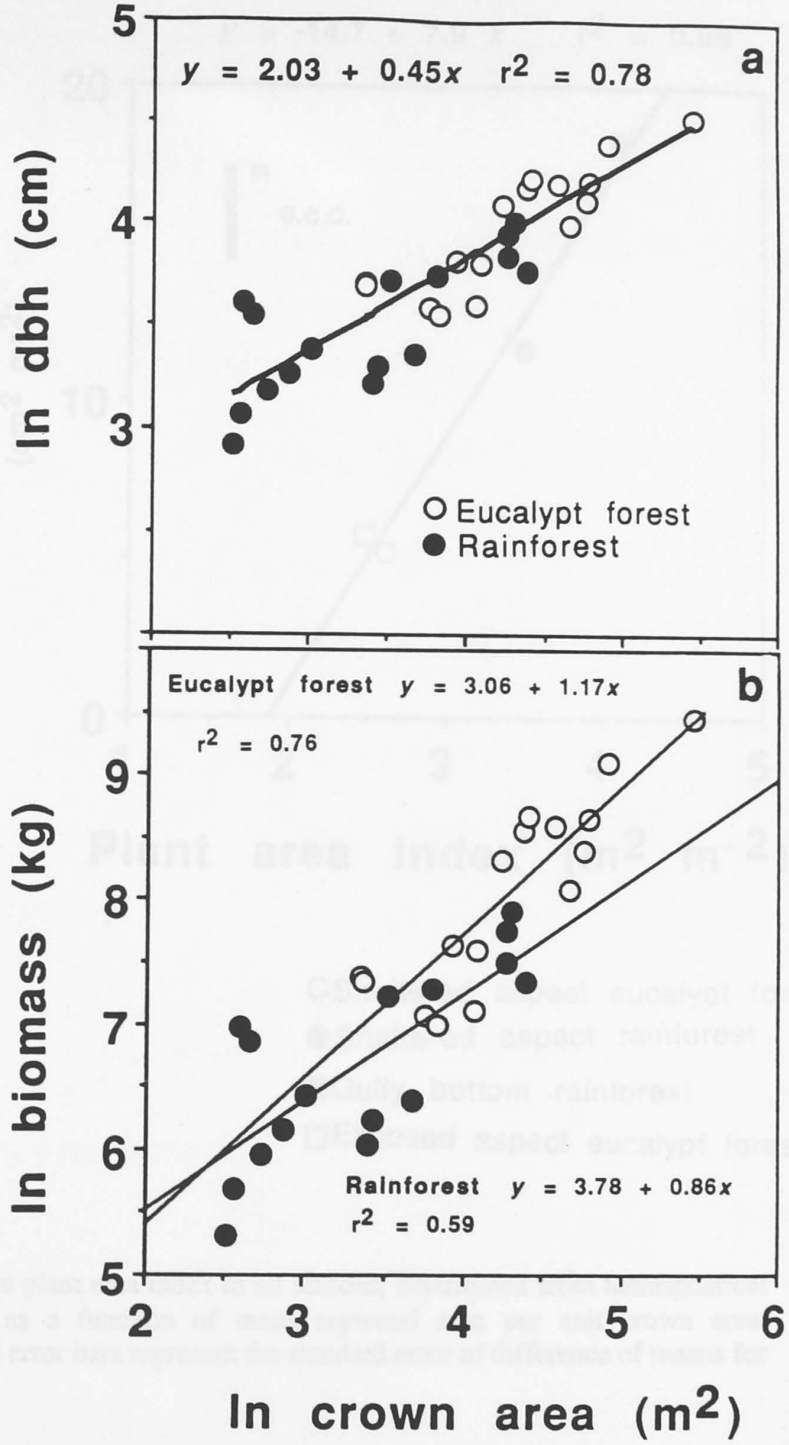


Figure 3.11. Allometeric relationships between (a) crown area and diameter at breast height, and (b) crown area and biomass, for eight trees each on four experimental plots in the Kioloa Flora Preserve southeastern New SouthWales.

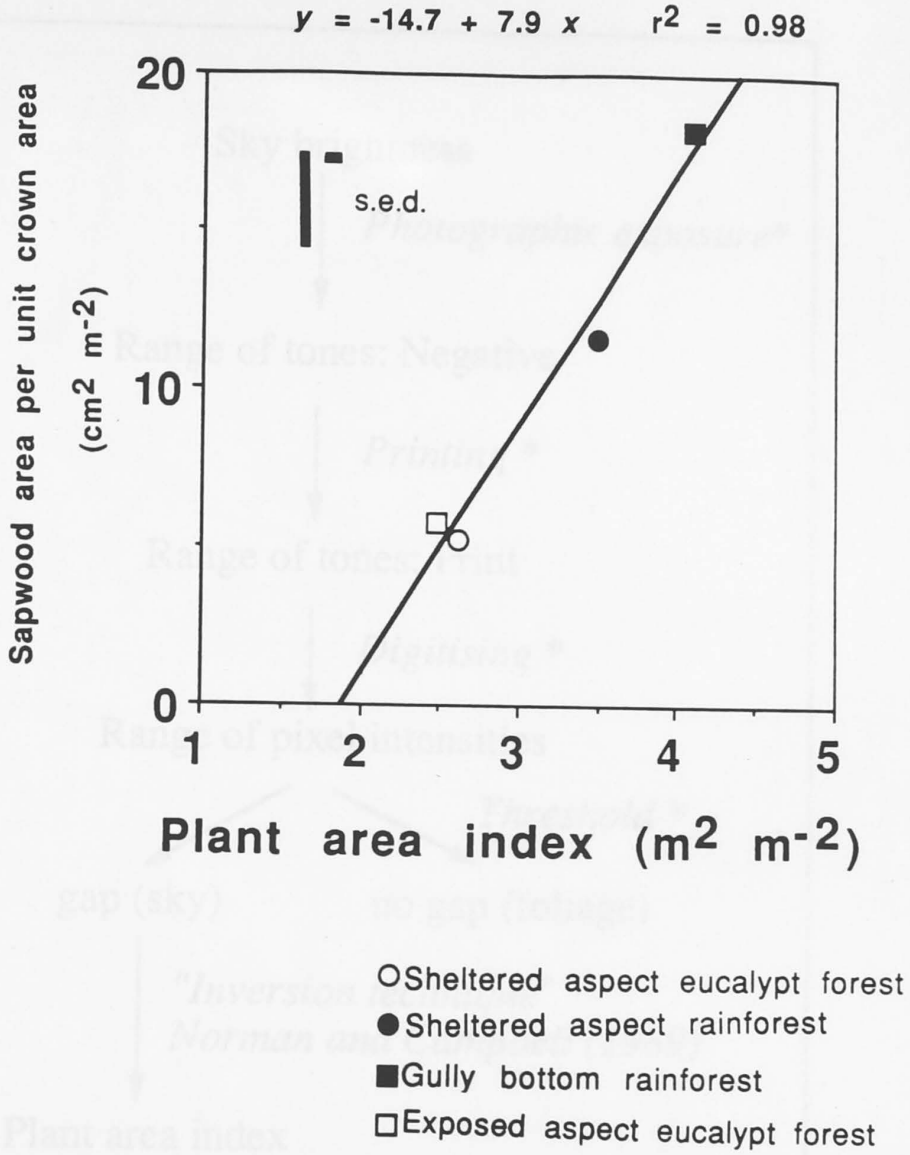


Figure 3.12. Mean site plant area index in all seasons, determined from hemispherical canopy photography, as a function of mean sapwood area per unit crown area. Horizontal and vertical error bars represent the standard error of difference of means for both variates.

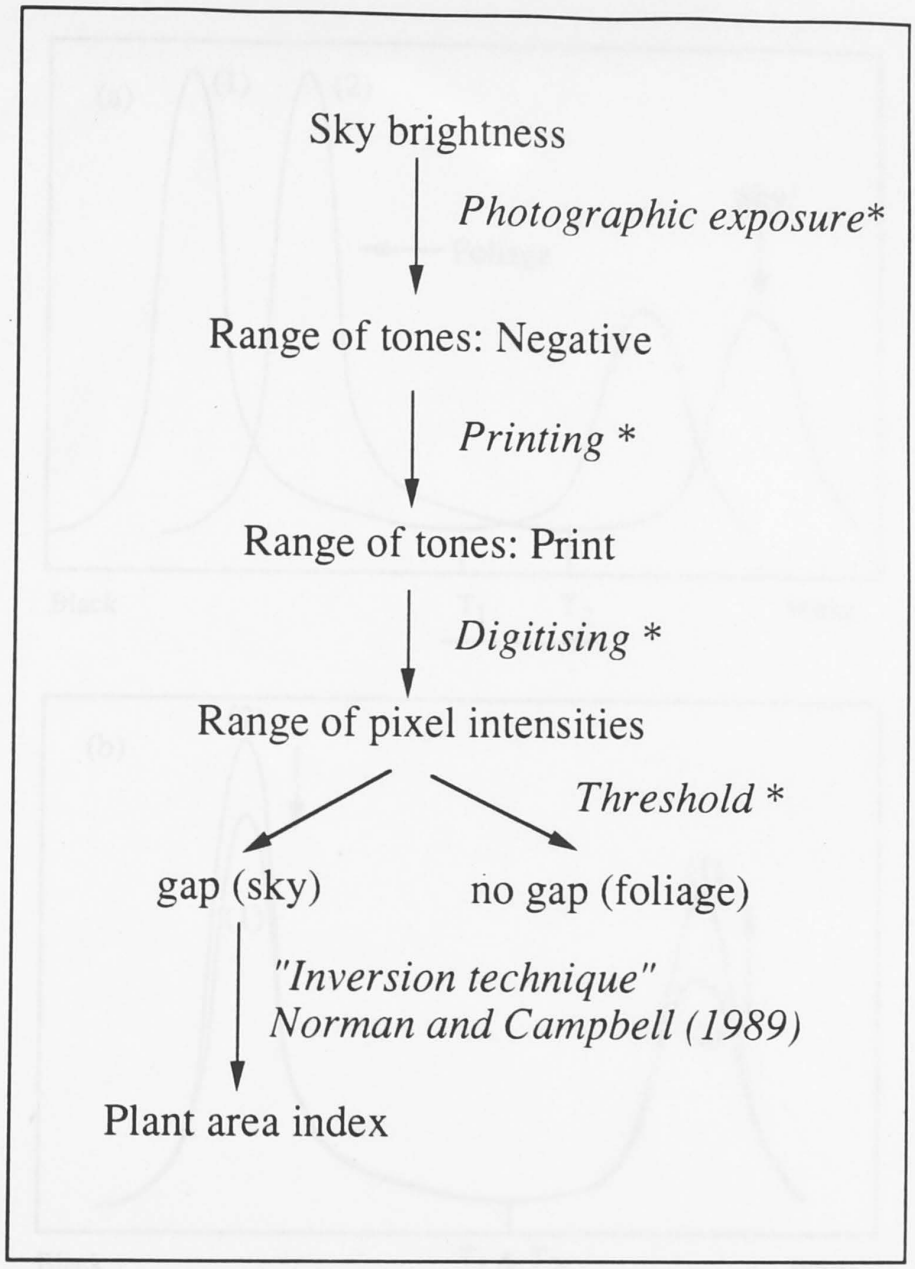


Figure 3.13. Schematic representation of procedure used to determine plant area index of forest canopies by the hemispherical photographic and image analysis technique. * indicates procedures which potentially bias the estimate of plant area index.

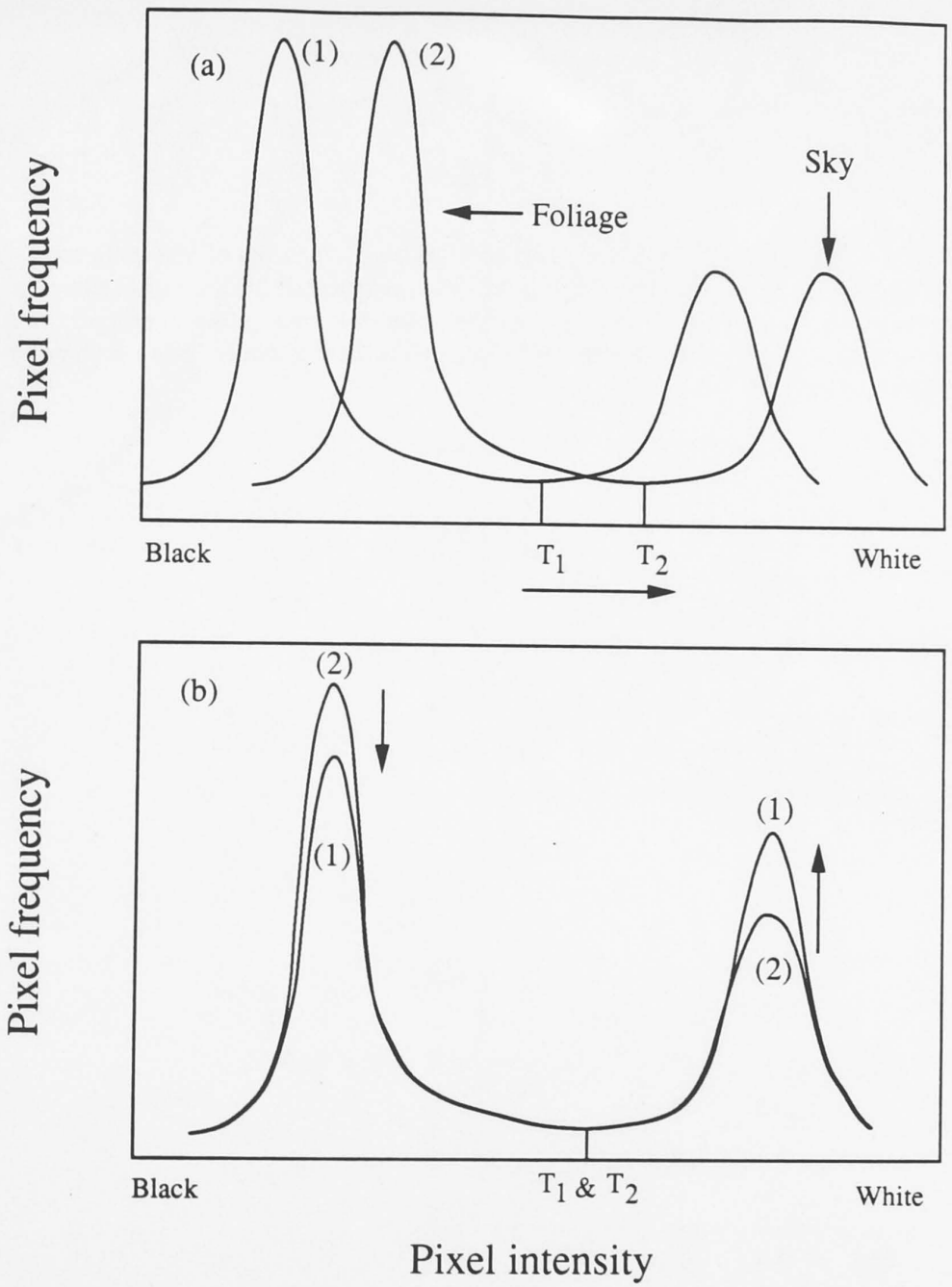
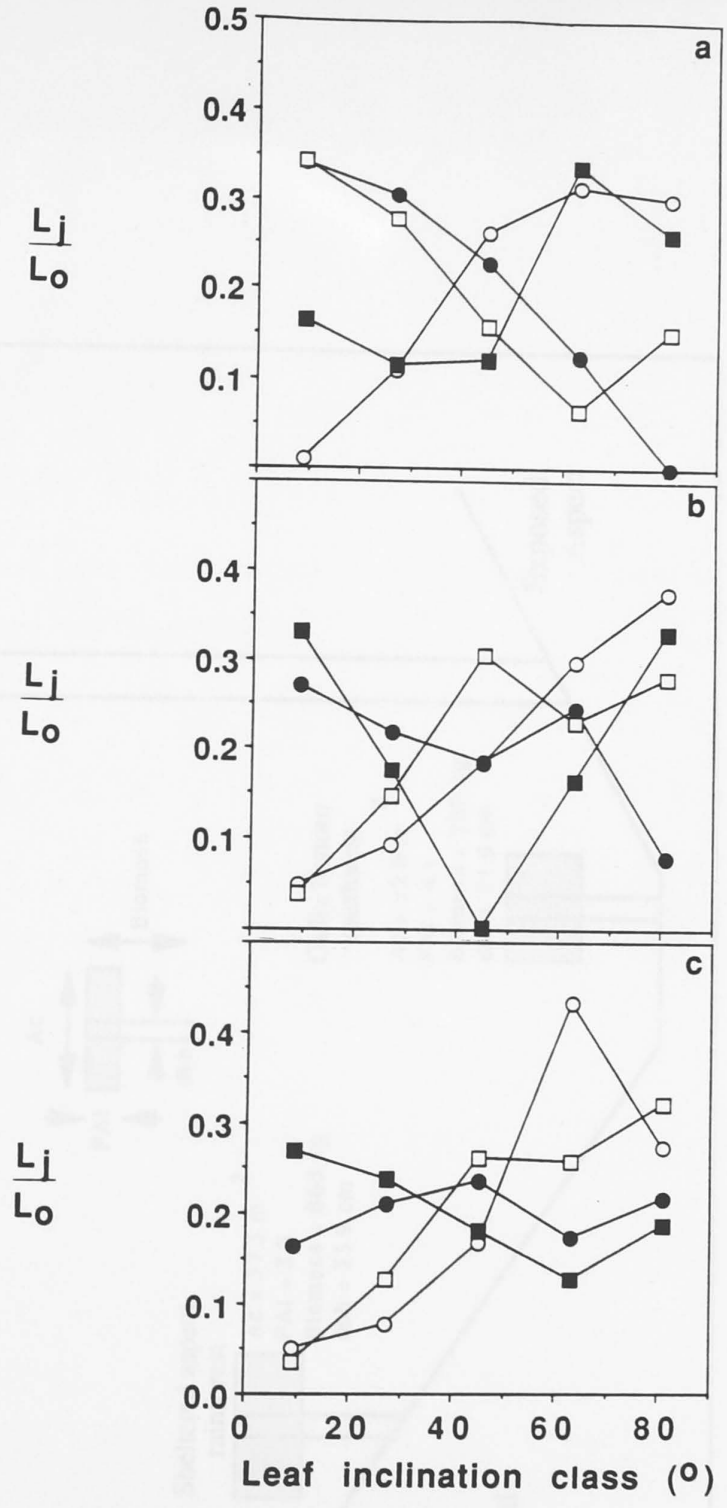


Figure 3.14. Schematic representation of the effect of photographic exposure on the pixel frequency histogram from hemispherical canopy photographs. (a) Variation in overall image intensity causes a shift in the frequency histogram, however, the relative difference between foliage and sky attributes remains constant. (b) Variation in the relative intensity of foliage and sky due to over or under exposure of image attributes. T_1 and T_2 represent threshold values separating foliage and sky image attributes.

Figure 3.15. Mean proportion of plant area index as a function of leaf inclination class for four plots at the field site. (a) winter, (b) summer, and (c) autumn measurements. Averages derived from 5 photographs per plot for each season, except for both rainforest and eucalypt forest sheltered aspect plots during winter, when 2 photographs per plot were used.


a
b
c
0.5
0.4
0.3
0.2
0.1
0.0
Lj/Lo
0
20
40
60
80
Leaf inclination class (°)
Sheltered aspect eucalypt forest
Sheltered aspect rainforest
Gully bottom rainforest
Exposed aspect eucalypt forest

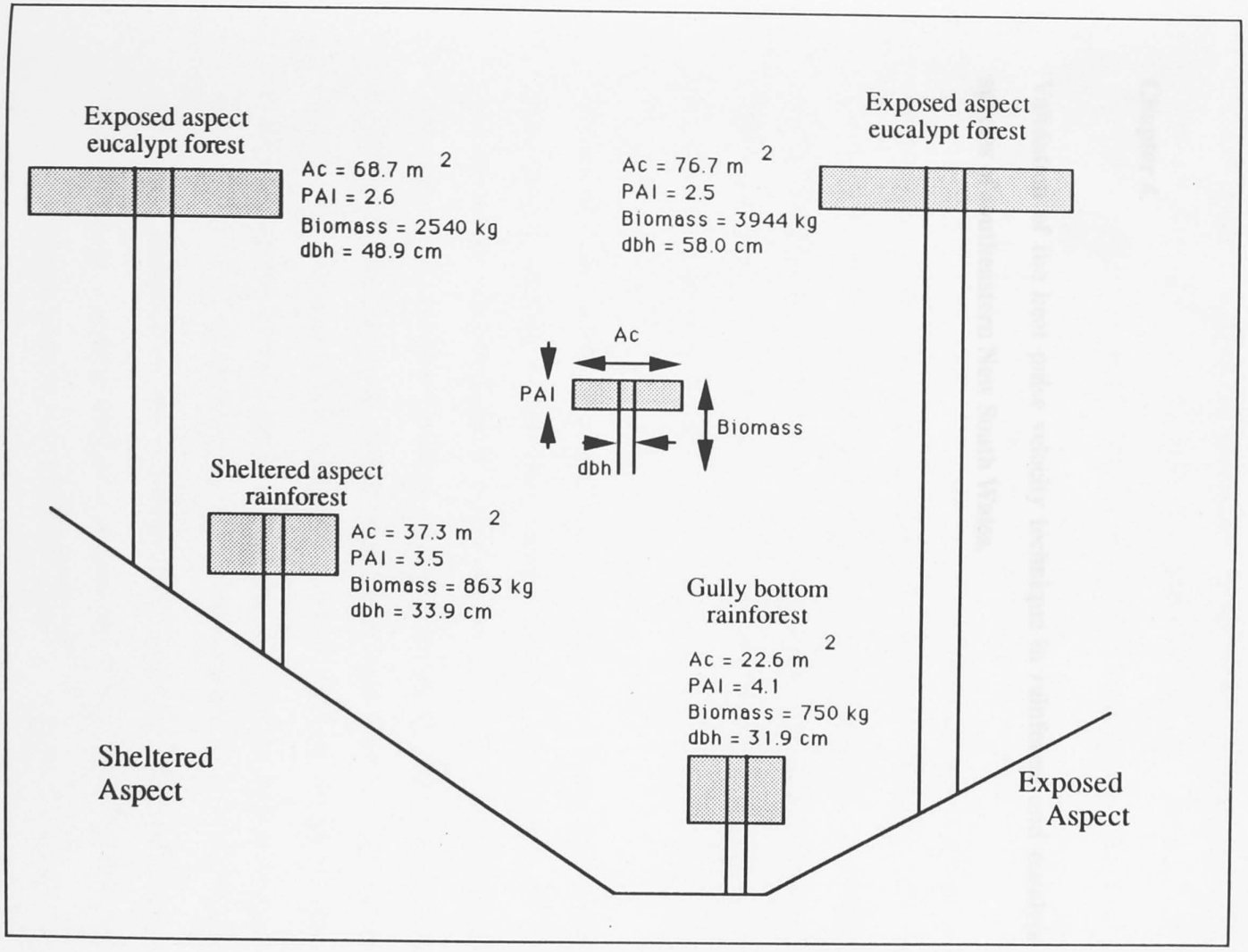


Figure 3.16. Schematic representation of mean tree characteristics (n = 8) in rainforest and eucalypt forest plots, located on sheltered and exposed aspects and the gully bottom, in a forested catchment in southeastern New South Wales.

Chapter 4.

Validation of the heat pulse velocity technique in rainforest and eucalypt forest species of southeastern New South Wales.

Abstract

Sap flow estimated by the heat pulse velocity technique was validated against water uptake from a potometer in two cut saplings each of *Eucalyptus maculata, Doryphora sassafras* and *Ceratopetalum apetalum*. Estimates of sap velocity were derived from measurements of the time, t_e, taken for equilibration of the temperature difference at two points in the sapwood after the initiation of a heat pulse. Sap flow was then calculated from estimates of sap velocity and measurements of sapwood area by dye uptake. Scanning electron microscopy revealed that the wound associated with drilling and placement of probes into the sapwood, was elliptical rather than circular as assumed in previous studies. However, the region of sapwood in which sap flow would be disrupted by probe placement, was equivalent to that of a circular wound of width comprising the drill hole (2.2 mm) and a lateral region each side, containing disrupted xylem vessels (0.3 mm). Consequently, a total wound width of 2.8 mm was used in calculations of sap flow.

The correspondence between instantaneous measures of sap flow derived from the heat pulse velocity technique, and time averaged water uptake from a potometer, was investigated by comparing linear regressions between each independent estimate of water use to a 1:1 relationship (slope = 1, y-intercept = 0). Sap flow measurements at high sap velocities and total sapling water use were similar between both heat pulse velocity and potometer techniques in five of the six saplings, consistent with previous studies. Departure of the slope from unity was attributed to error associated with the measurement of t_e. Largest errors in the measurement of t_e occurred at low sap velocities. Deviation of the y-intercept from zero was attributed to error in the measurement of constants used to calculate sap flow. These constants were: (1) measured distances between heater and each temperature probe, (2) measured sapwood moisture content and density, and (3) estimated sapwood area. Sapwood area was suggested as the major source of error in the estimation of sap flow as the boundaries

between sapwood and heartwood tissues were not always clearly defined, and also due to squaring of any error associated with measurement of the inner and outer radii of conducting tissue. Sapling water use summed over the experimental period, was largely composed of measurements at high sap velocities when errors associated with the measurement of t_e were relatively low. Nocturnal sap flow, at low velocities, contributes little to overall total sapling water use. These results suggested that reliable estimates of diurnal variation in sap flux and total water use in trees of these species *in situ* may be obtained using the heat pulse velocity technique.

Introduction

The heat pulse velocity technique was conceived by Huber (1936, cited in Marshall 1958) as a method of measuring sap velocity in plant stems. When a heat pulse is initiated at a point in the sapwood, sap velocity determines the change in temperature at any point. Thus, the sap velocity (cm h^{-1}) may be calculated from measurements of the rate of change of temperature. These data, together with conducting tissue area, can then be used to estimate sap flux (kg h^{-1}). This technique represents a convenient method of measuring water use in tall trees, since all water transpired from the canopy must pass through the trunk. This chapter describes the results of a validation experiment in which measurements of sap flow, by the heat pulse velocity technique, were compared with sap flow measured by the uptake of water in cut saplings.

Theory.

A theoretical derivation of the one-dimensional movement of a heat pulse emanating from a perpendicular linear heat source in a stationary matrix occupied by moving sap streams, was developed from the differential equation describing conduction of heat in a homogeneous isotropic solid, by Marshall (1958). Marshall showed that the

temperature at a point in the matrix, after the heat pulse was initiated, was determined by conduction of heat through the wood and forced convection of the heat pulse by moving sap (Fig. 4.1a). The convection term was, therefore, directly related to sap velocity. Sap velocity could be calculated from the temperature taken at three time intervals at a single point downstream from the heat source. Closs (1958) simplified the technique by solving the same differential equation for two temperature sensors, one placed at a distance upstream and a second downstream of the heat source. The heat pulse velocity, V_h, was inversely proportional to the time taken for the temperature differential between the two sensors to return to zero (t_e, seconds),

$$V_h = \frac{x_1 + x_2}{2t_e} \qquad (4.1)$$

where x_1 and x_2 (cm) are distances to temperature sensors upstream and downstream, respectively, from the heat source. In the present study, x_1 and x_2 were 0.5 and 1.0 cm, respectively. Convection of the heat pulse is perturbed by the presence of the heater and temperature probes and the disruption of the xylem tissue associated with their placement (Fig. 4.1b). Consequently, the heat pulse velocity must be corrected for wounding,

$$V_h' = a + bV_h + cV_h^2 \qquad (4.2)$$

where V_h' is the corrected heat pulse velocity (cm s^{-1}) and the coefficients a, b and c were derived by Swanson and Whitfield (1981) from numerical solutions of Marshall's (1958) equations for various wound sizes. Sap flux (V_s) is calculated from corrected heat pulse velocity as,

$$V_s = V_h' \frac{\rho_b (C_w + mC_s)}{\rho_s C_s} \qquad (4.3)$$

where C_w and C_s (J g^{-1} $^oC^{-1}$) are the specific heat capacity of dry wood and sap (water), respectively, ρ_b (kg m^{-3}) is the basic density of dry wood, ρ_s (kg m^{-3}) is the density of sap (water), and ***m*** (kg water kg^{-1} wood dry weight) is the moisture fraction of the sapwood (Marshall 1958; Closs 1958; Swanson and Whitfield, 1981)

Sap flow (Q) may be calculated by integration of the radial sap velocity profile around the tree bole (Swanson 1975; Edwards and Warwick 1984; Cohen, Fuchs and Green 1981; Green and Clothier 1988; Edwards 1992). Alternatively, sap flow may be calculated from sap velocity weighted by the area of sapwood most closely associated with each point temperature measurement (Hatton *et al.* 1990),

$$Q = \Sigma \pi (r_i^2 - r_{i+1}^2) V_s \qquad (4.4)$$

where r_i and r_{i+1} are the outer and inner radii of an annulus of sapwood most closely associated with the i^{th} temperature sensor. The latter method was used in the present work.

In this chapter the heat pulse velocity technique is validated for rainforest and eucalypt forest species from southeastern New South Wales, by comparison with independent measurements of water use. Rates of water uptake by cut saplings in a potometer were compared to estimates of sap flux derived from measurements of t_e and sapwood area. The species studied were *Ceratopetalum apetalum* and *Doryphora sassafras*, as representative of the rainforest, and *Eucalyptus maculata* as representative of the eucalypt forest. These three species co-occur in southeastern New South Wales, and were used in a field study to investigate *in situ* whole tree water use in relation to variation in microenvironment (Chapter 5).

Methods

Wound response.

The wounding of sapwood tissues caused by drilling and probe implantation incorporated mechanical disruption of xylem vessels, vessel blockage by compounds produced by sapwood in response to exposure to air, and the introduction of petroleum jelly into the drill hole. Measurement of the wound width of each species was determined from sapwood hand sections under both light microscope, at 40X magnification, and scanning electron microscopy, using the procedures outlined in Exley *et al.* (1974), Exley *et al.* (1977) and Kucera (1981).

Heat pulse velocity.

Heat pulse velocity in both cut saplings and whole trees (see Chapter 5) was determined using equipment manufactured by CSIRO, Division of Water Resources (Durham and Hatton 1989). Two temperature probes were constructed of sealed Teflon tubing, 2.2 mm diameter, each containing two 4-10 Ω glass encapsulated thermistors (Thermometrics, New Jersey, USA), separated by either 0.5 or 1.5 cm distance. Each temperature probe was placed in the conducting tissue 0.5 cm upstream and 1.0 cm downstream from a 2.0 mm diameter heater probe. Sapwood area of trees for the field study were determined in Chapter 3 (Table 3.2). The heater probe was constructed of stainless steel tubing and nichrome wire (5.5 $\Omega\ m^{-1}$ @ 20° C, Driver Harris, Australia). A heat pulse was produced every 15 minutes by supplying a 2.5 second, 12 volt, 3.3 ampere current from a lead acid battery along a 15 or 25 m cable to the heater probe. This voltage increased the heater temperature by 10-15°C above ambient. Holes for temperature (2.2 mm diameter) and heater probes (2.0 mm diameter) were drilled to a depth of up to 100 mm with a battery powered drill. A drill guide was utilised to ensure

parallel alignment of drill holes into the sapwood. Petroleum jelly facilitated insertion of probes and maintained thermal contact between probe and sapwood. The trunk around the temperature and heater probes was shielded from direct sunlight by aluminium foil taped to the trunk. A data logger recorded the time interval between initiation of a heat pulse and equilibration of the temperature difference between upstream and downstream temperature probes (t_e in equation 4.1). Digital information from a voltage/frequency converter connected to each thermistor, was transferred *via* 15 or 25 meter coaxial cables to the data logger, which was later accessed by an MS-DOS microcomputer (Toshiba T1200). Sap flux every 15 minutes, was calculated using equations 4.1 - 4.4 in a Microsoft Excel spreadsheet.

Wood density and moisture content of the sapwood for saplings and trees, were measured from samples removed using a 4 mm increment corer. Samples were immediately placed in pre-weighed micro-Eppendorf tubes and sealed. Wood volume was determined by water displacement of fresh samples. Wet and dry weights were determined before and after drying samples for 24 hours at 110°C. Wood density, ρ_b, was calculated from the ratio of dry weight to wood volume. Wood moisture fraction, m, was calculated from the ratio of weight of water in the wood sample to wood dry weight.

Validation of the heat pulse velocity technique.

Saplings of *E. maculata, D. sassafras* and *C. apetalum* between 2.5 and 6 m high, and between 1.8 and 6.3 cm dbh, were cut from Kioloa State Forest and used in a potometer experiment in the same manner as Roberts (1977). Sap flow measured by water uptake from a beaker was compared with that calculated by the heat pulse velocity technique. Two saplings of each species were cut from the forest and transported in darkness to either the Australian National University Field Station, Kioloa, or enclosed in plastic

and immediately transported to a glasshouse in Canberra, two hours drive away. The cut stem of the sapling was placed in a large container of water and then recut underwater 10 - 15 cm higher, to exclude air emboli from xylem vessels. The sapling was suspended in a beaker of water on a 15kg Mettler electronic balance. Evaporation from the beaker was prevented by applying a film of cooking oil on the water surface. Water uptake by the sapling was automatically recorded from the balance every 15 minutes by computer while measurements of sap velocity were recorded simultaneously with the heat pulse velocity equipment. Heater and thermistor probes were implanted in the sapwood at approximately 20 cm above the beaker, but below the first branch. Following measurements of water use, sapwood tissue was identified; Schiff's Reagent was added to the potometer water and the sapling continued transpiring until sufficient reagent had been taken up to stain xylem vessels pink. Conducting tissue area was measured by taking a transverse section of the stem and estimating the area of stained xylem tissue. Sap flow was calculated from the product of sapwood area and sap velocity (equation 4.4).

Results

Wound response.

The wound due to probe implantation was investigated by light and scanning electron microscopy. Under the light microscope, transverse hand sections through the drill hole revealed that the wound comprised three components: (a) that due to removal of wood by the drill bit, (b) that due to mechanical disruption of vessels at the edge of the drill hole, and (c) that due to blockage and discolouration of xylem vessels adjacent to the wound. Another aspect of the wound was revealed by examination of tangential sections under scanning electron microscopy (Fig. 4.2 and 4.3), which showed that vessels directly above and beneath the drill hole were twisted with rotation of the drill

bit causing longitudinal damage up to 0.85 mm from the edge of the drill hole (Fig. 4.4). The extent of lateral wounding, up to 0.3 mm, agreed with measurements made under the light microscope. This lateral damage appeared to be due to crushing of vessels and rays resulting in blockage of conducting tissue. The nature and extent of the damage was similar in all species.

The total wound width, 2.8 mm, was calculated as the sum of the drill hole (2.2 mm) and twice the lateral wound width (2 x 0.3 mm) for all species. Coefficients *a, b* and *c* in equation 4.2, were calculated as 1.524, 0.964 and 0.124 by Swanson and Whitfield (1981) for a wound width of 2.8 mm. These values were used to determine V_h' from which sap flux was calculated.

Validation of the heat pulse velocity technique.

Sap flow, determined by weight loss from the potometer and by the heat pulse velocity technique, agreed well at high sap velocities but differed at low sap velocities (Fig. 4.5). At low sap velocities, the heat pulse velocity and consequently also sap flux, were overestimated. This result was consistent with previous studies (Swanson and Whitfield 1981; Lopushinsky 1986; Jones *et al.* 1988). At low sap velocity, forced convection of the heat pulse by sap flow becomes less than heat conduction by the sapwood resulting in a systematic overestimation of heat pulse velocity. The velocity where heat pulse and potometer curves separate in Fig. 4.5 (indicated by arrows) represents the minimum reliably measured sap flux by the heat pulse velocity technique in each species. Thus, at sap velocities less than 15.7, 10.9 and 9.4 cm h^{-1} for *E. maculata, C. apetalum* and *D. sassafras*, respectively, sap flow could not be measured accurately. By considering that the heat pulse velocity = 0 at sap velocities less than the minimum measureable sap

flow, diurnal patterns of sap flow more closely approximated those measured by the potometer (Fig. 4.6, 4.7 and 4.8). In some cases, oscillations were apparent in the heat pulse measurements at low sap flux (eg. Fig. 4.6b and 4.7b).

In all species, sap flow determined by both techniques increased after sunrise, reached maximum values near midday and declined during the afternoon to minimum values at night. Diurnal variation in sap flux calculated by both techniques appeared to correspond in each sapling. There was a linear relationship between sap flow measured by the heat pulse velocity technique, and rates of water uptake from the potometer (Figs. 4.9, 4.10 and 4.11). However, in some cases, the slope and y-intercept was significantly different from the 1:1 relationship (slope = 1, y-intercept = 0), although, this variation was not systematic between species. Both "*C. apetalum* 2" and "*D. sassafras* 2" saplings (Fig. 4.9b and 4.10b) transported to Canberra had significantly lower slope and higher y-intercept than a 1:1 line ($P < 0.05$). Additionally, the y-intercept of "*E. maculata* 1" sapling (Fig. 4.11a) transported to the Kioloa Field Station was greater than zero ($P < 0.05$). All other regression lines were not significantly different from a 1:1 relationship between both techniques.

To remove the influence of the large number of records with low sap flow, the regression analyses were repeated on data collected between 8:00 and 17:00 hours (Table 4.1). In all cases the slope of the regression equation was not significantly different from a 1:1 relationship, except for one sapling ("*C. apetalum* 2"). Additionally, y-intercepts were not significantly different from zero in all saplings, except for the rainforest saplings transported to Canberra. Evidently data at low sap flow were the major cause of the departure from a 1:1 relationship in Figs. 4.9-4.11. Estimates of total water use by the heat pulse velocity technique differed from measured weight loss from the potometer by less than 7% (Table 4.2). Additionally, there were no systematic differences in total water use between species.

Discussion

Wound response.

Drilling holes for probe emplacement into the sapwood produced an elliptical rather than a circular region of wounding around the drill hole. The dimensions of the wound were up to 0.85 mm longitudinal to the stem axis, and 0.3 mm on the transverse axis. Such an elliptical wound may result from a shearing stress imparted to the vertical ends of the vessel elements by drill torque, thereby twisting and crushing xylem vessels as observed in Fig. 4.2. The dimensions of the wound were similar in all species. The lateral wounding was stained dark brown, possibly due to oxidation of wood tissue or deposition of phenolic compounds on contact with air (Marshall 1992). In their numerical solutions, Swanson and Whitfield (1981) assumed that the wound caused by probe emplacement was circular. They showed that interruption to sap flow in the vicinity of implanted probes caused an underestimate of true sap velocity by the heat pulse velocity technique. In the present study, in which the wound was elliptical, the transverse rather than longitudinal wound width, would seem to have predominant influence on disrupting sap flow and perturbing heat pulse convection. Thus, it was considered appropriate that the coefficients for *a, b* and *c* in equation 4.2 were taken from Swanson and Whitfield (1981) for a transverse wound width of 2.8 mm. Marshall (1992) showed empirically that a doubling of the transverse wound width, caused an error of between 40 and 70% in the estimated sap flux. However, agreement between each measure of water use in the present work (Figures 4.9 - 4.11) supports the choice for using the transverse wound width as a measure of the total wound. This transverse wound width was somewhat smaller than wound widths measured by Marshall (1992) using light microscopy. He reported values of 3.1 mm in *E. marginata, E. camaldulensis* and *E. globulus* for a drill width of 1.8 mm, due to tylose formation in vessels. No evidence for tylose formation was observed in the present work. This may

be due to the relatively short period in which drill holes were used for measurements (2 days), rather than weeks by Marshall (1992).

Validation of heat pulse velocity technique.

At zero sap velocity, conduction of the heat pulse by wood and stationary sap will produce a finite, but large value for t_e. Consequently, the heat pulse velocity calculated in equation 4.1 will always be a finite value and the corrected heat pulse velocity (V_h') will approach the value of *a* in equation 4.2. Thus, sap velocity is overestimated at low sap flow using the heat pulse velocity technique. Swanson and Whitfield (1981) showed from numerical solutions of equation 4.1, that significant errors in measurements of heat pulse velocity occured at sap velocities below 3 cm h^{-1}. Somewhat better resolution has been reported by Lassoie *et al.* (1977) and Lopushinsky (1986) with minimum measurable sap velocities of 1.8 and 1.9 cm h^{-1}, respectively. The results from the present study suggested that at sap velocities of 15.7, 9.4 and 10.9 cm hr^{-1} for *E. maculata, D. sassafras* and *C. apetalum*, respectively, the sap flow estimated by the heat pulse velocity technique departed from that measured by potometer water uptake. These minimum measureable sap velocities were greater than those reported by Lassoie *et al.* (1977), Swanson and Whitfield (1981) and Lopushinsky (1986), and may be due to differences in wood anatomy and/or temperature probe construction. The structure and distribution of tracheids in conifer sapwood may more closely approximate the idealised sapwood, used in the original derivation by Marshall (1958). The theoretical case applies to thin parallel capillaries through which sap flow occurs at a constant velocity. Xylem vessels in angiosperms, however, tend to be wider than tracheids (Zimmermann 1983), possibly causing departure in practice from the idealised case. Alternatively, the sensitivity of the temperature probe to changes in sapwood temperature may be affected by probe construction. Swanson and Whitfield (1981) used glass thermistors probes, whereas

Lassoie *et al.* (1977) and Lopushinsky (1986) used stainless steel probes. In the present study, the low thermal conductivity, k, of air (k_{air} 2.6 x 10^{-4} J s^{-1} cm^{-1} $^{o}K^{-1}$) between the teflon probe wall (k_{teflon} = 2.5 x 10^{-3} J s^{-1} cm^{-1} $^{o}K^{-1}$) and the glass encapsulated thermistor (k_{glass} = 1.2 x 10^{-2} J s^{-1} cm^{-1} $^{o}K^{-1}$) may reduce thermistor sensitivity to changes in wood temperature at low sap velocities; the air effectively insulating the thermistor from small variations in temperature in the sapwood. Increased sensitivity of the temperature probe may have been achieved by injecting epoxy resin to exclude air from the probes or using probe materials of high thermal conductivity in direct contact with the thermistor, such as stainless steel (k_{steel} = 1.6 x 10^{-1} J s^{-1} cm^{-1} $^{o}K^{-1}$) as was used by Jones *et al.* (1988).

Arbitrarily assinging a zero heat pulse velocity for values below the minimum measureable sap flow mayappreciably underestimate flow during prolonged periods of low sap velocity. Additionally, slight variation in actual sap flow around the minimum measureable sap velocity may produce apparent oscillations in sap flux displayed in Figures 4.6b and 4.7b, rather than true variation in sap flow. These oscillations disappear at sap velocities greater than the minimum measureable sap velocity because forced convection of the heat pulse is much larger than conduction. Thus, estimates of sap velocity by the heat pulse velocity technique are more reliable at high sap flux (Swanson and Whitfield 1981; Jones *et al.* 1988).

Sap flow was calculated as the product of sap velocity and sapwood area measured by dye uptake. From transverse sections of the stem of each sapling, it was observed that the dye was not evenly distributed either radially or tangentially throughout the sapwood (see also Legge 1985; Cermak *et al.* 1992). Thus, sap velocity varies with both depth into the sapwood and with position around the stem (Swanson 1975; Lassoie *et al.* 1977; Miller *et al.* 1980; Hatton and Vertessy 1989; Dye *et al.* 1991; Dunn and Connor 1991; Cermak *et al.* 1992). The measurement of heat pulse velocity by a single temperature sensor applies only to vessels within the region adjacent to that sensor

(Marshall 1958; Jones *et al.* 1988). Consequently, reliable estimation of sap flux in large trees may require multiple sampling points dispersed throughout the sapwood (Dye *et al.* 1991). In cut saplings, however, estimation of instantaneous sap flow derived from only two point measurements of sap velocity, produced reliable estimates compared with time averaged measurements of water uptake from the potometer, particularly at high flow rates (Table 4.1). Departures from the 1:1 relationship were, in many cases, due to low sap velocities resulting in error in the estimation of heat pulse velocity (Figures 4.9 - 4.11). Deviations of the slope from unity suggest that errors were dependent on sap velocity. Thus, slopes significantly different from one are due to error associated with t_e. Such errors occur at low sap velocities as explained above. Removal of low values from the analysis improved the slope comparison (Table 4.1). Additionally, variation in slope may be due to error in the measurement of wound width, but an error of this type was not evident in the present study because it would cause a curvilinear relationship between heat pulse velocity and potometer measurements due to non-linearity in equation 4.2.

In contrast to the departure of the regression slope from 1, deviation of the y-intercept from zero suggests an error associated with measurement of one of the constants used to measure sap flux. These include: (1) inacurate alignment of drill holes, which may lead to errors in x_1 and x_2 in equation 4.1, (2) error in measurement of wood moisture content or wood density in equation 4.3, and (3) error in measurement of the inner and outer radii of conducting tissue used to calculate sapwood area in equation 4.4. Significant departures of the y-intercept from zero in both saplings "*C. apetalum* 2" and "*D. sassafras* 2" (Table 4.1) may be due to error associated with measurement of one of these constants. The error associated with measurement of sapwood width may potentially be the most significant as these errors are squared in the calculation of sapwood area. For example, in a tree of 40 cm dbh under the bark, and sapwood width of 3 cm, a 0.5 cm error in measurement of the inner radius of sapwood (r_{i+1} in equation 4.4) may result in an error of up to 16% in estimated sap flux.

Total sap flow was calculated from the integration of sap flux over a 24 hour period. During this period, error associated with low sap velocities (ie. at night) is relatively small. Consequently, the difference in sap flux measurements between both techniques was between 1% and 7% (Table 2). These estimates of total water use by water uptake and the heat pulse velocity technique are similar to results obtained for *Pinus halepensis* (2% difference), *Pinus radiata* (4% difference), *Nothofagus solandri* (9% difference to estimates made by water vapour diffusion in a cuvette) by Swanson and Whitfield (1981), in apple trees (7% difference) by Green and Clothier (1988), and in *Eucalyptus grandis* (between 7 and 12.7% difference) by Olbrich (1991) and Dye *et al.* (1992).

This validation experiment demonstrated that, at high sap flow rates, reliable estimates of instantaneous water use were obtained using the heat pulse velocity technique in cut saplings of *E. maculata, D. sassafras* and *C. apetalum*. Additionally, reliable estimates of total water use were obtained by intergration of sap flux over a 24 hour period. It was assumed that, by utilisation of the techniques outlined in this chapter, reliable estimates of sap flux may be obtained in canopy trees of these species in a forested catchment in southeastern New South Wales (Chapter 5).

Table 4.1.

Linear regression coefficients for the relationship between sap flow estimated by the heat pulse velocity technique and that measured by water uptake, for measurements made between 8:00 and 17:00 hours. Data derived from Figures 4.6, 4.7 and 4.8 for *Ceratopetalum apetalum, Doryphora sassafras* and *Eucalyptus maculata*, respectively. d.f. = degrees of freedom. CI = 95% confidence interval for the estimate of slope and y-intercept.

Sapling	d.f.	slope	CI	y-intercept	CI
C. apetalum (1)	51	1.00	0.10	0.0004	0.0103
C. apetalum (2)	25	0.80+	0.11	0.0140*	0.0099
D. sassafras (1)	38	0.92	0.14	0.0126	0.0187
D. sassafras (2)	60	0.88	0.12	0.0173*	0.0152
E. maculata (1)	36	0.92	0.13	0.0426	0.0446
E. maculata (2)	8	0.80	0.78	0.0030	0.0120

+ = slope significantly different from unity

* = y-intercept significantly different from zero.

Table 4.2.

Total sapling water use over the experimental period, in litres (L), measured by water uptake from the potometer (ΣQ_P) and the heat pulse velocity technique (ΣQ_H) in two cut saplings of *C. apetalum, D. sassafras* and *E. maculata* from the Kioloa State Forest. Percentage differences were based on the assumption that the total water uptake from the potometer was the true value.

Sapling	ΣQ_H (L)	ΣQ_P (L)	% difference
C. apetalum (1)	1.90	1.84	+3
C. apetalum (2)	0.91	1.07	-7
D.sassafras(1)	2.00	1.96	+2
D.sassafras(2)	1.35	1.29	+5
E.maculata(1)	3.06	2.94	+4
E.maculata(2)	0.08	0.08	-1

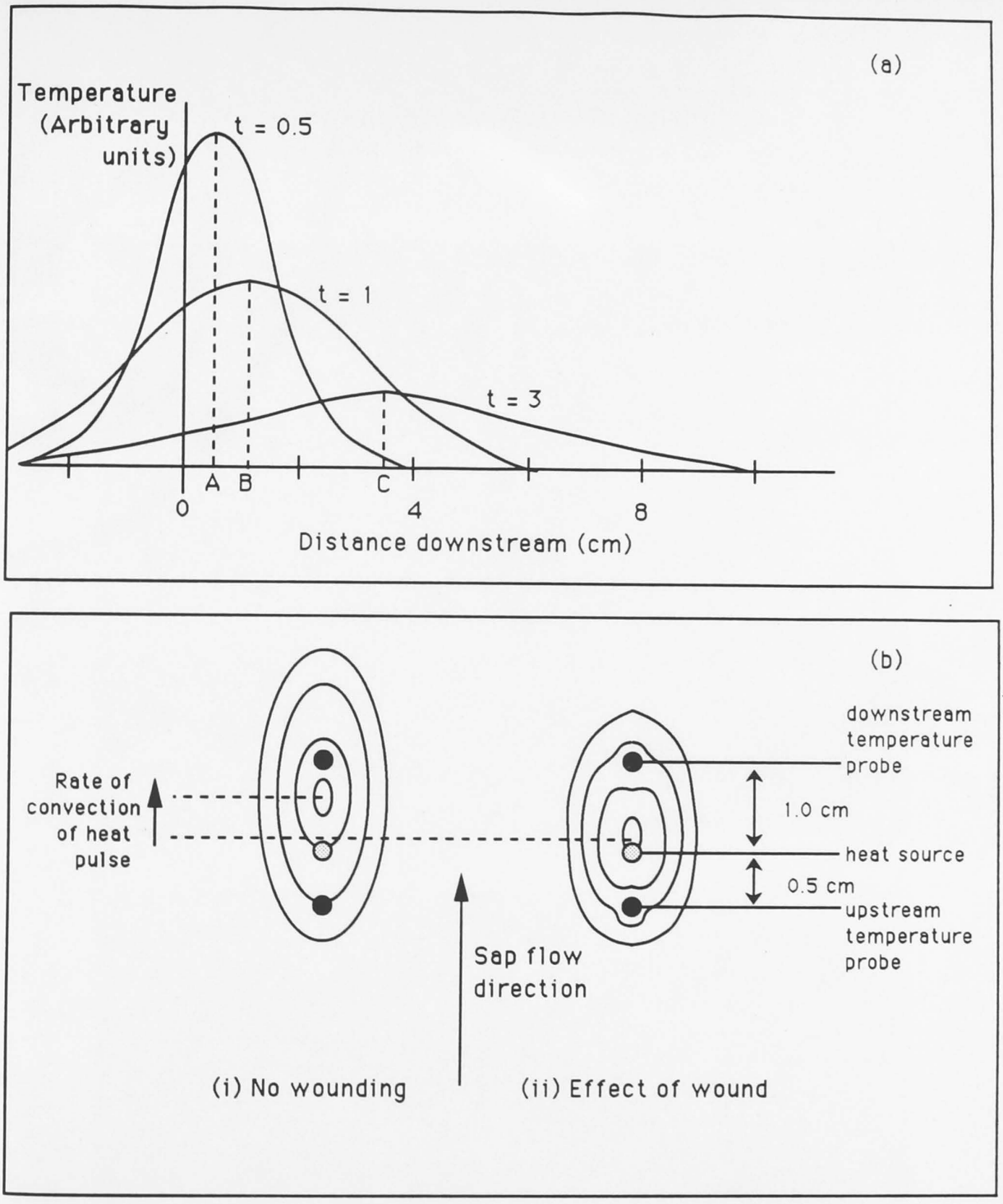


Figure 4.1. (a) Theoretical temperature distribution as a function of distance downstream from the heater probe, adapted from Marshall (1958). Each curve represents the temperature distribution at a particular time, t (minutes). Heat pulse velocity =70 cm h^{-1}. Points labelled A, B and C represent the center of the heat pulse for each t. The distance between the heater probe and each of A, B and C is determined by forced convection of the heat pulse by moving sap. Spreading of the curve is due to conduction of heat by the wood/sap matrix. (b) Isotherms at an instant in time for the convection of a heat pulse within a moving sap stream, for (i) no wound, and (ii) wounding due to probe implantation of temperature and heater probes (adapted from Swanson and Whitfield 1981). Wounding causes distortion of isotherms in regions near probes and a reduction in the rate of convection of the heat pulse.

Figure 4.2. Scanning electron micrographs of the wound response in *Ceratopetalum apetalum*. Similar observations were made for other species. (a) Tangential section of drill hole. Arrow indicates region below drill hole in which tissue damage has occurred due to drill torque (up to 0.85 mm). (b) Enlarged view of (a) showing shearing and compression of vessels due to drill torque.

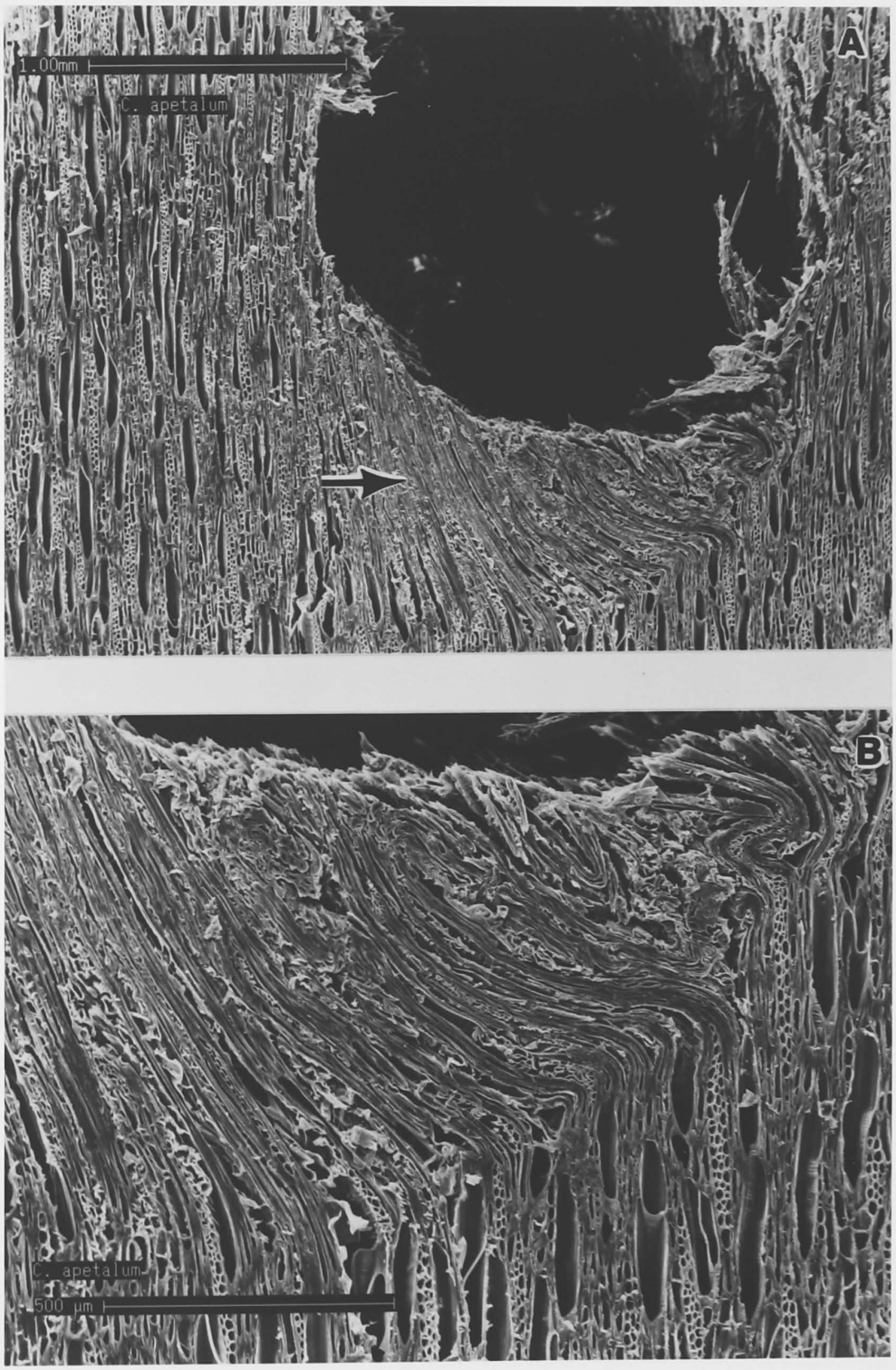
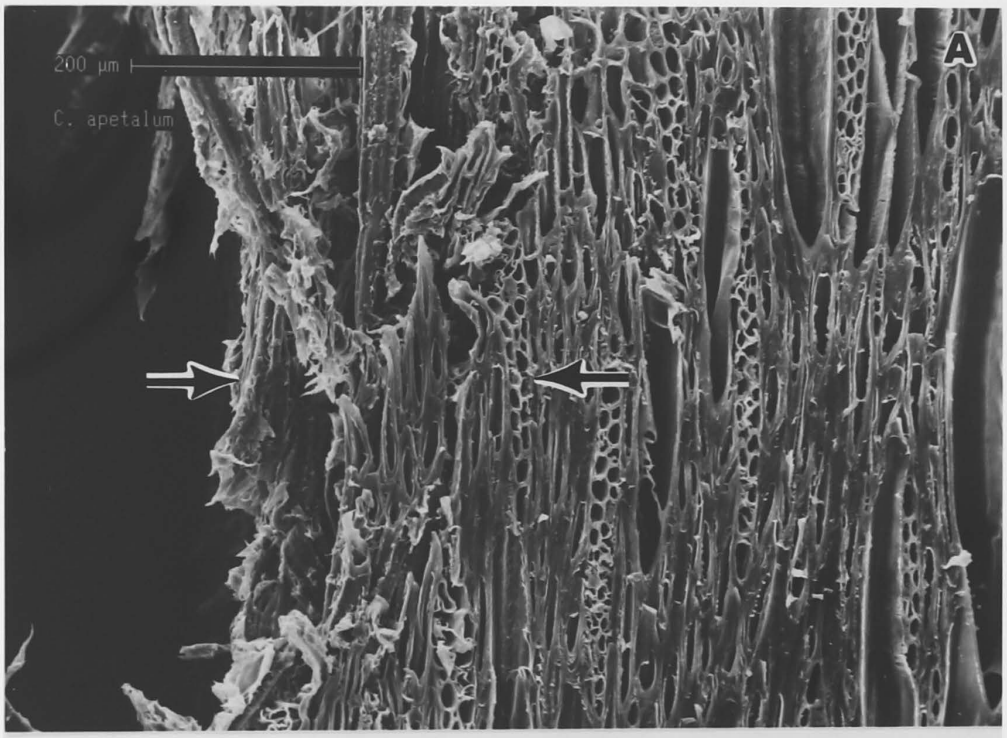
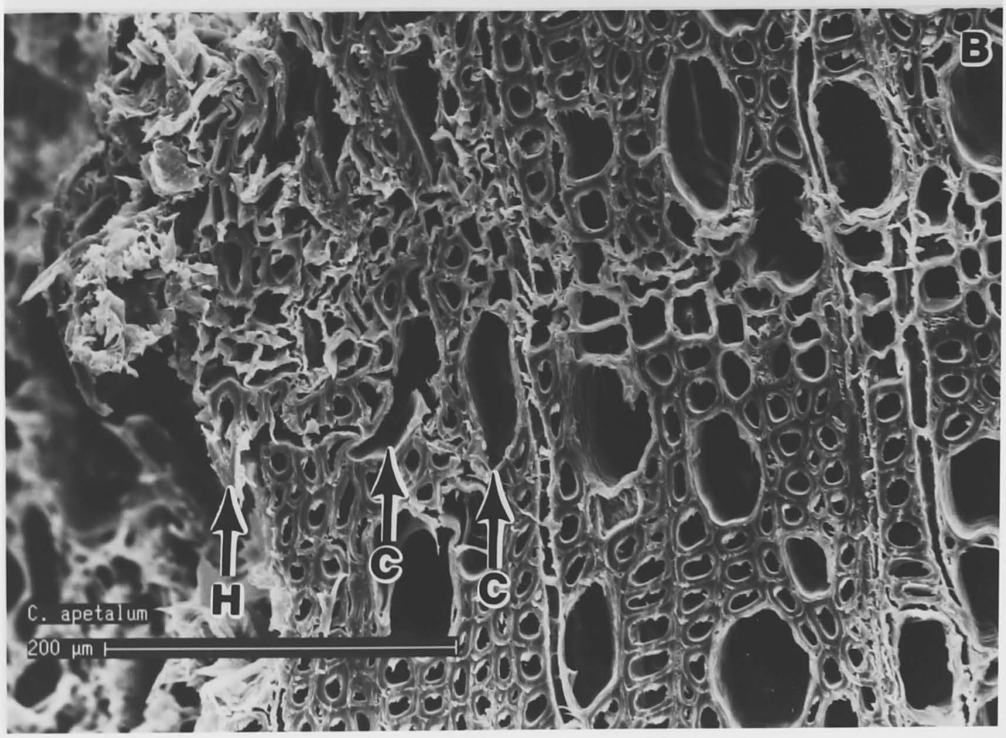

A
1.00mm
C. apetalum
B
C. apetalum
500 µm

Figure 4.3. Scanning electron micrographs of the wound response in *Ceratopetalum apetalum*. (a) Lateral wound response, showing crushed vessels and wood rays in a region 0.3 mm wide, bounded by arrows. Intact xylem vessels and wood rays occur outside this region. (b) Transverse section at edge of drill hole (H at lower left) showing crushed (C) and intact vessels to the right.


200 µm
C. apetalum
A


B
H
C
C
C. apetalum
200 µm

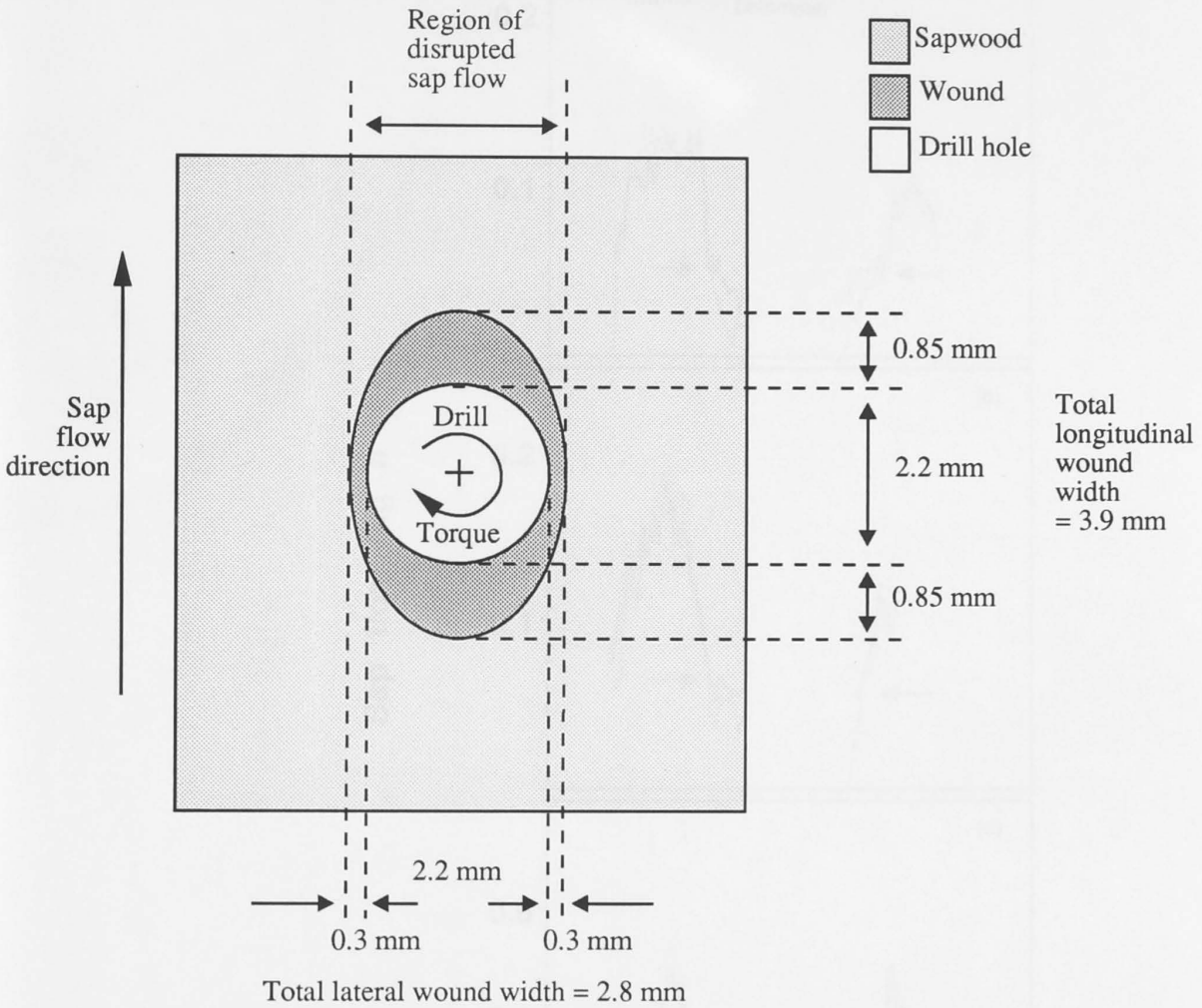


Figure 4.4. Schematic representation of wounding caused by drilling and temperature probe implantation. An elliptical wound results from drill torque imparting a shearing stress on vertically aligned xylem vessels. Consequently, the vertical wound width (0.85 mm) was greater than the lateral wound width (0.3 mm). No differences were observed between species.

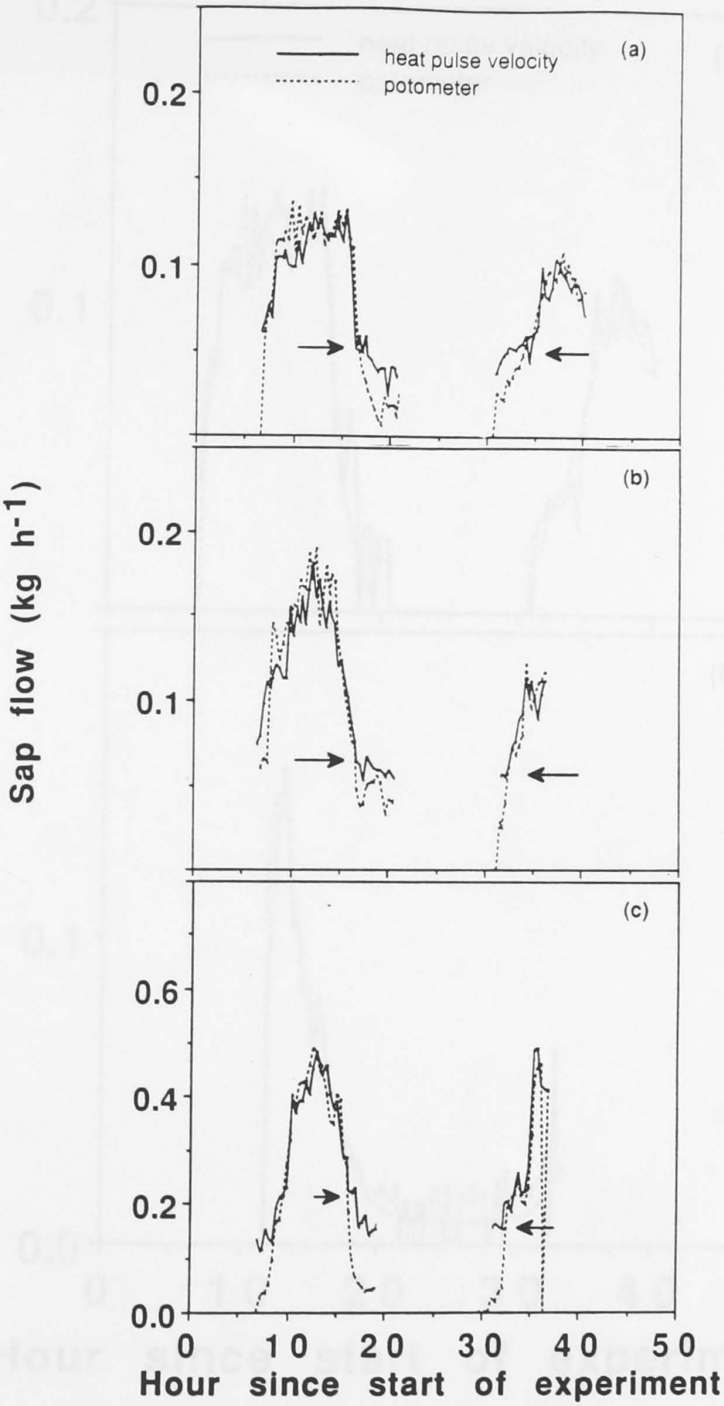


Figure 4.5. Sap flow in one cut sapling of each species estimated by both potometer (dashed line) and heat pulse velocity techniques (solid line). Arrows indicate departure of estimated sap flow by the heat pulse velocity technique from the measured uptake of water from the potometer. This result was due to an overestimation of heat pulse velocity at low sap velocities. All saplings were cut from the Kioloa State Forest and transported immediately to the Kioloa Field Station; (a) *Ceratopetalum apetalum*, collected 25-June-1991, (b) *Doryphora sassafras*, collected 16-June-1991, and (c) *Eucalyptus maculata*, collected 27-June-1991.

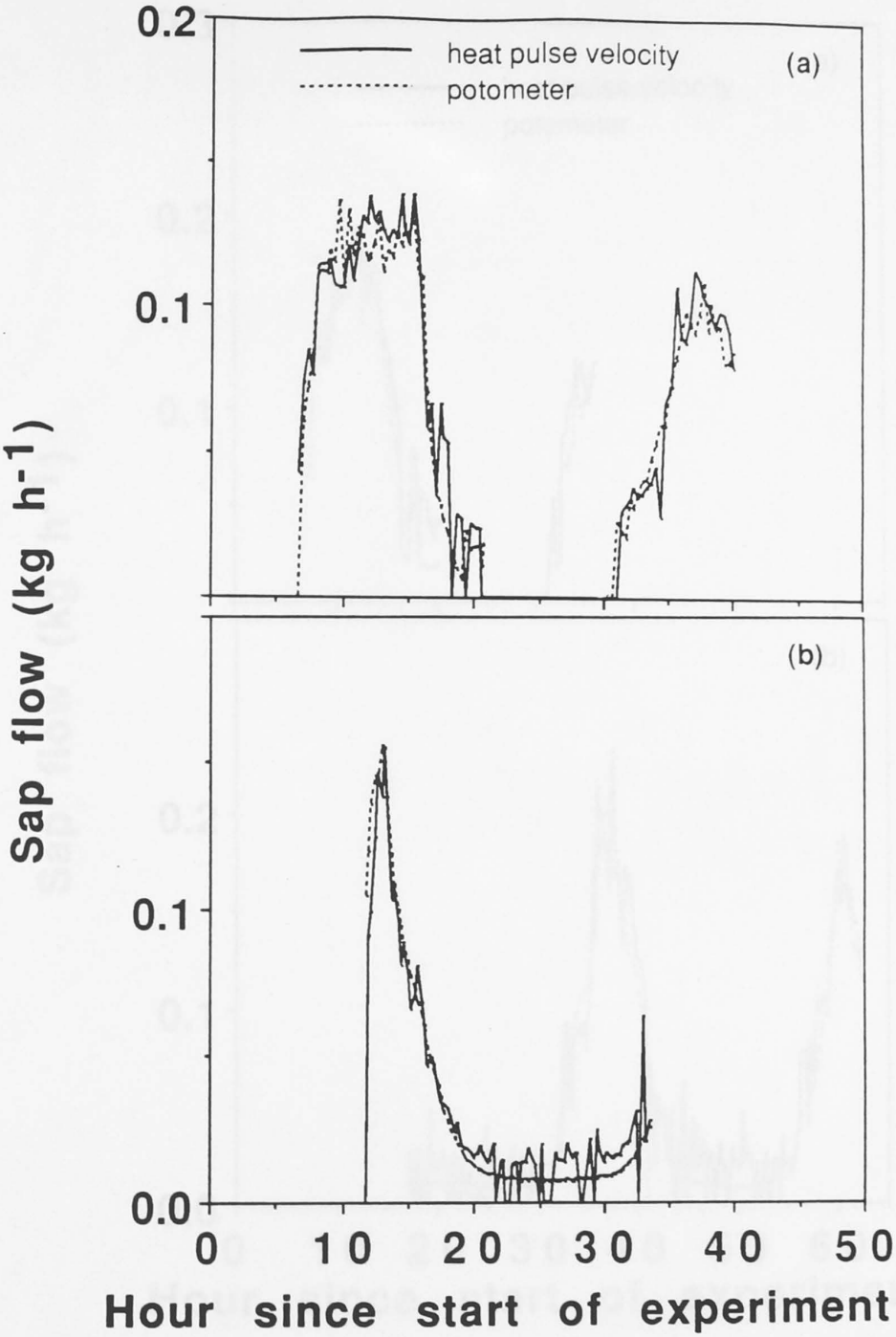


Figure 4.6. Comparison of sap flow in cut saplings of *Ceratopetalum apetalum* measured simultaneously by water uptake (dashed line) and heat pulse velocity technique (solid line), corrected for bias at low sap velocities as described in the text. Saplings were collected from the Kioloa State Forest on (a) 25-June-1991 (2.8 cm dbh), then transported to the Kioloa Field Station, and (b) 1-May-1992 (2.5 cm dbh), then transported immediately to Canberra and measured under glasshouse conditions.

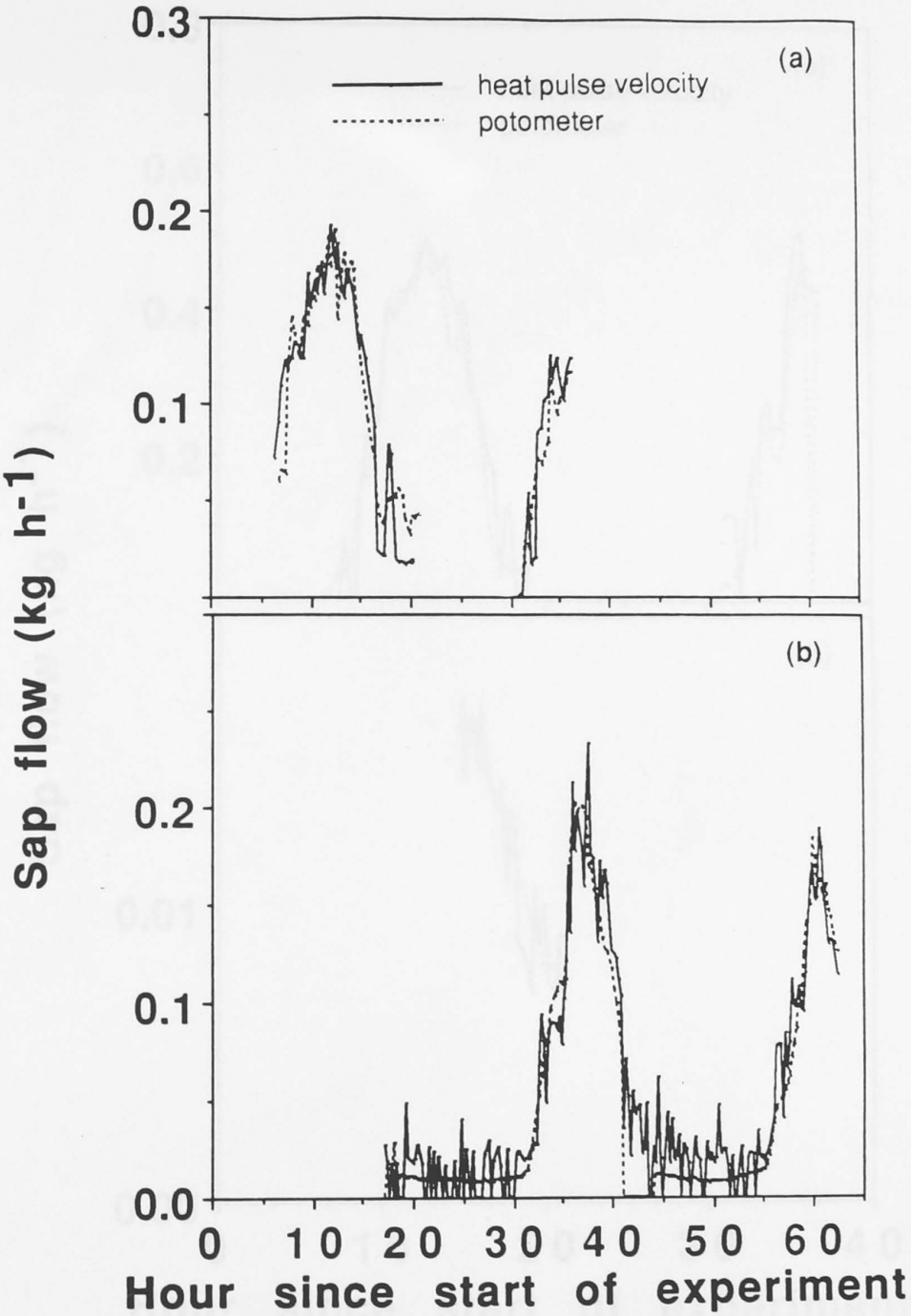


Figure 4.7. As in figure 4.6, but for *Doryphora sassafras*. Saplings collected (a) 16-June-1991 (4.5 cm dbh), then transported to Kioloa Field Station, and (b) 9-May-1992 (2.6 cm dbh), then transported to Canberra and measured under glasshouse conditions.

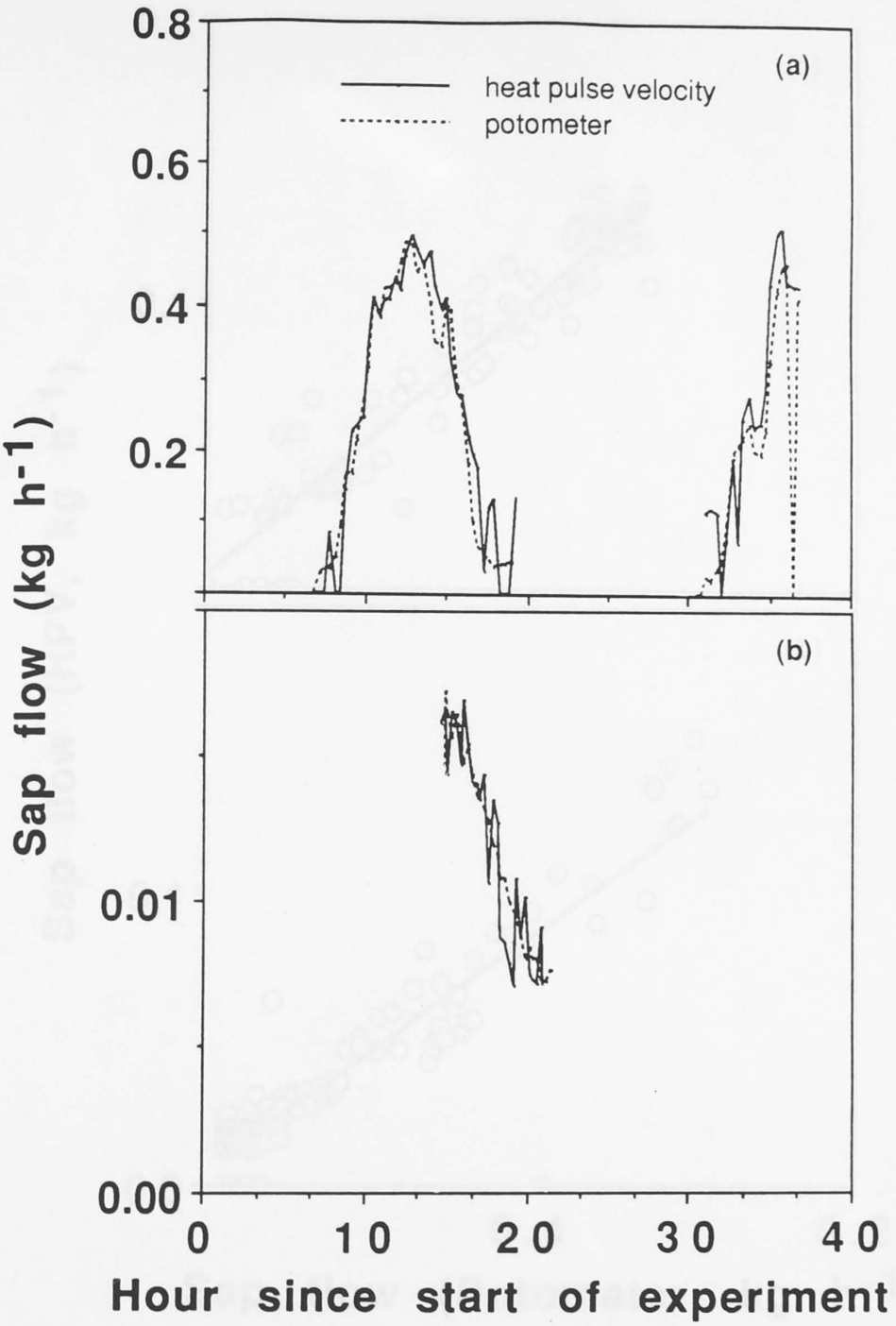


Figure 4.8. As in Figure 4.6, but for *Eucalyptus maculata*. Saplings collected (a) 27-June 1991 (6.3 cm dbh), then transported to Kioloa Field Station, and (b) 1-March-1992 (1.8 cm dbh), then transported to Canberra and measured under glasshouse conditions.

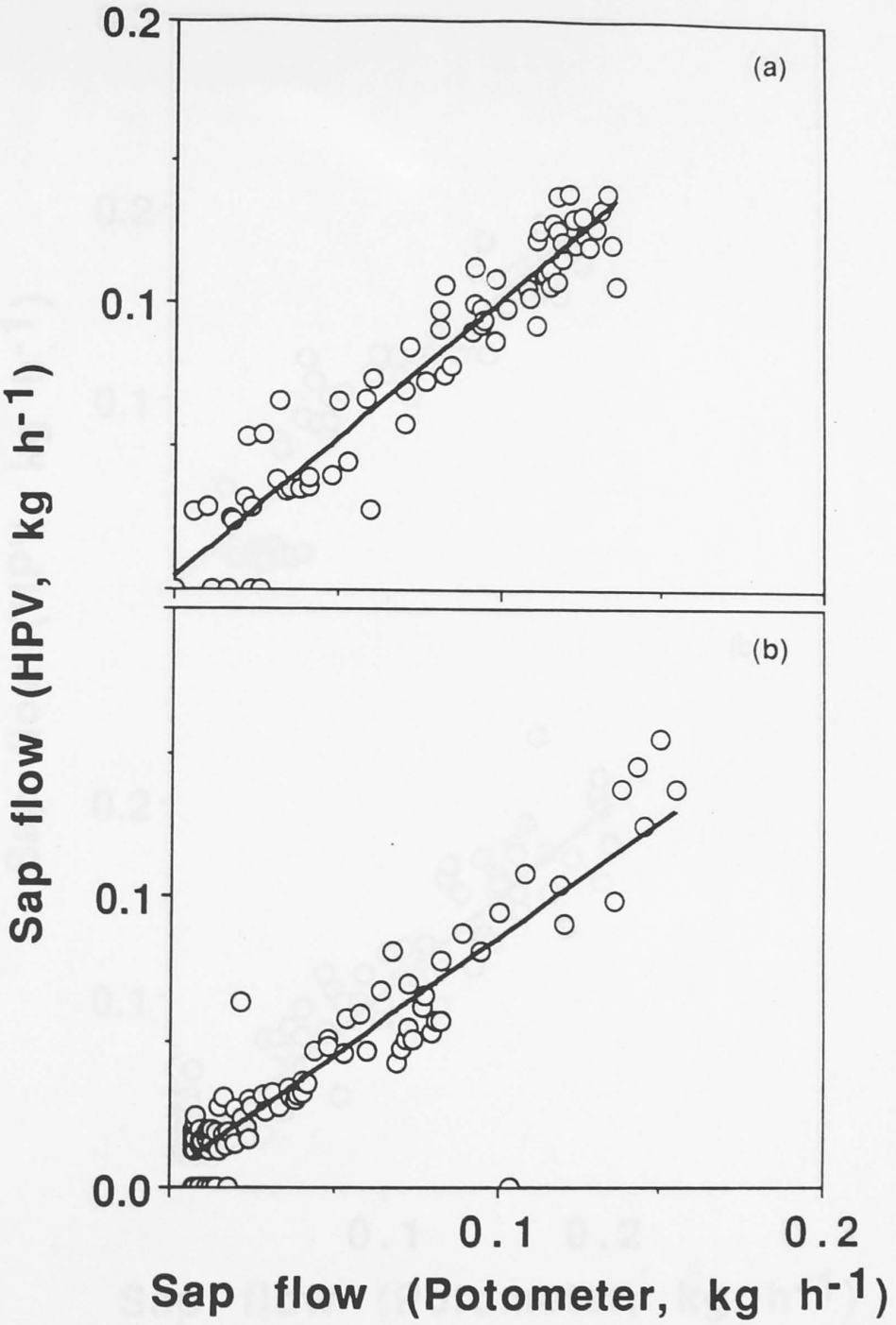


Figure 4.9. Relationship between sap flow measured by water uptake from the potometer and heat pulse velocity (HPV) technique in two cut saplings of *Ceratopetalum apetalum* from the Kioloa State Forest. Diagonal line represents the linear regression calculated for all data replotted from Figure 4.6.

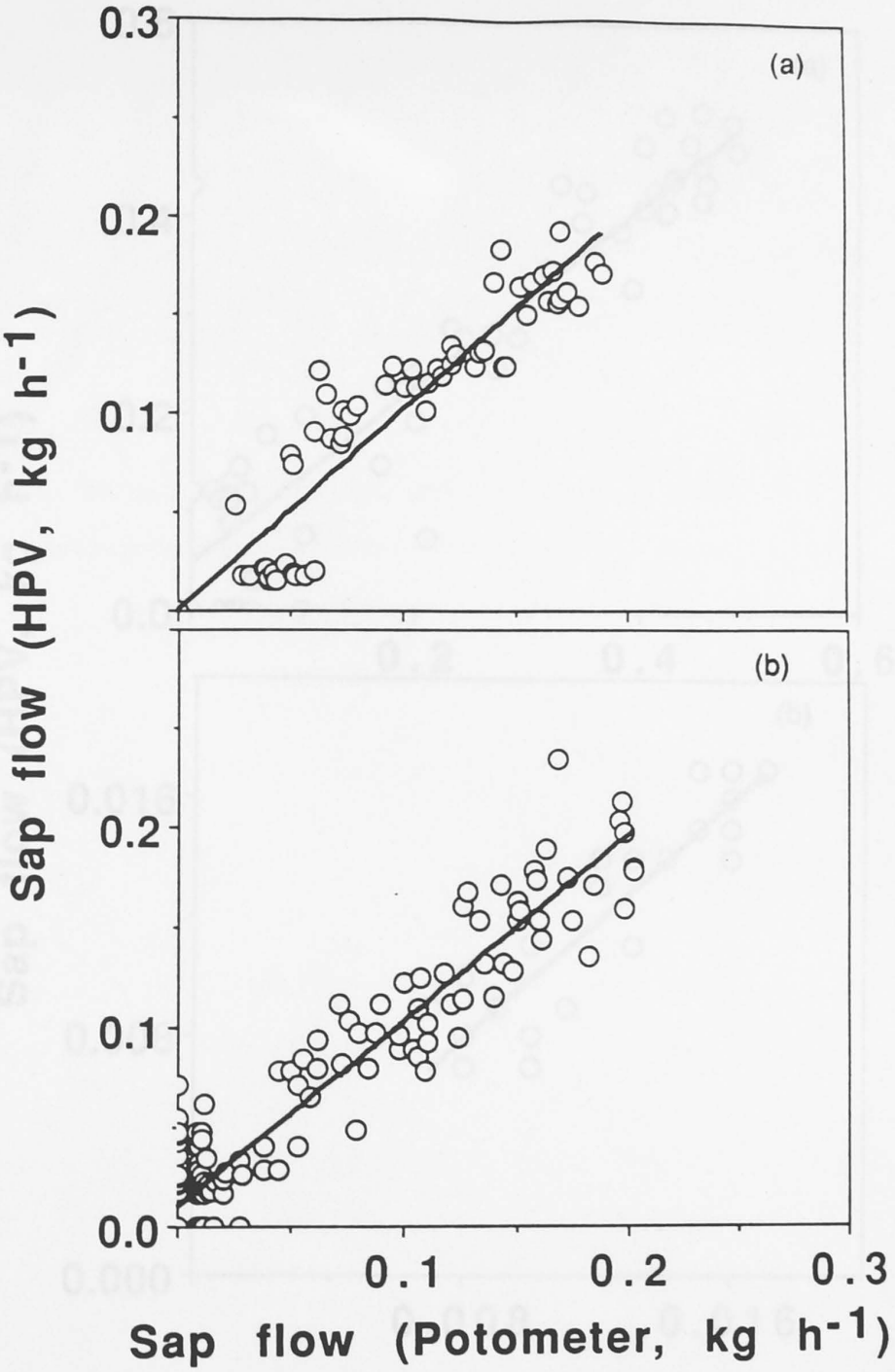


Figure 4.10. As in Figure 4.9, but for *Doryphora sassafras*.

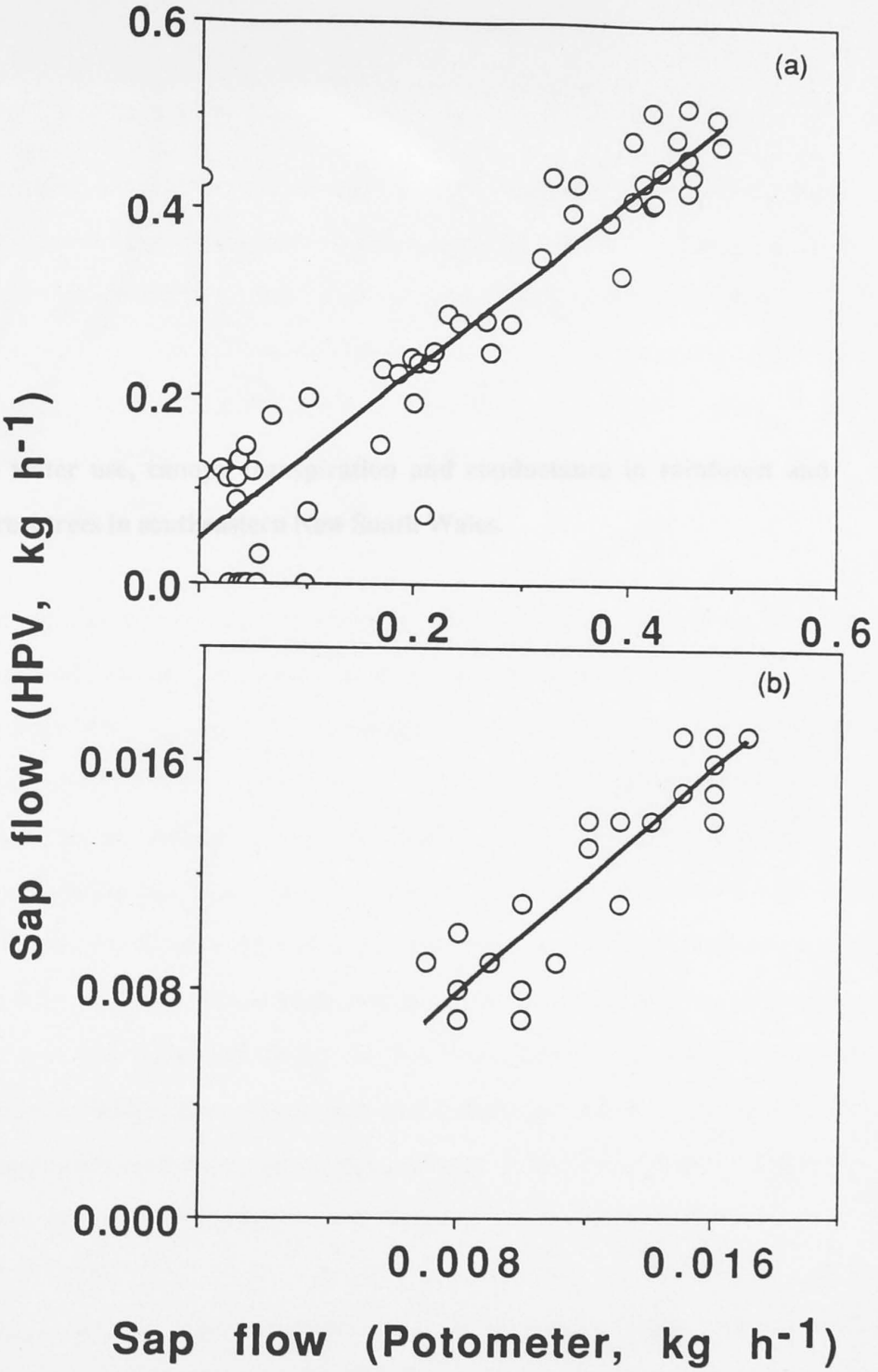


Figure 4.11. As in Figure 4.9, but for *Eucalyptus maculata*.

Chapter 5

Whole tree water use, canopy transpiration and conductance in rainforest and eucalypt forest trees in southeastern New South Wales.

Abstract

The heat pulse velocity technique was used to investigate whole tree canopy transpiration and canopy conductance to water vapour in rainforest and eucalypt forest vegetation on sheltered and exposed aspects in southeastern New South Wales. Sap flow was measured in eight *Eucalyptus maculata* trees on each of two eucalypt forest plots, and in four trees of *Doryphora sassafras* and *Ceratopetalum apetalum* on each of two rainforest plots, over two week periods in winter and summer 1991, and autumn 1992.

Maximum sap flow was linearly related to sapwood area in both forest types, but for a given maximum sap flow, sapwood area was lower in eucalypt forest trees than in rainforest trees. This suggested that *E. maculata* may have a lower internal resistance to water transport through xylem vessels, than rainforest trees. Diurnal canopy transpiration rate per unit crown area in all species, was more strongly coupled to variation in humidity and canopy conductance throughout the middle of the day, than to variation in global irradiance. In all seasons, mean maximum canopy transpiration rate was greater in rainforest at the gully bottom, than upslope in either rainforest or eucalypt forest. In winter and autumn, higher transpiration rates were attributed to greater water availability due to downslope lateral drainage. However, during summer, higher transpiration rates were due to higher canopy to air vapour pressure difference and a greater leaf area index in rainforest at the gully bottom.

High canopy conductances per unit crown area in the early morning generally decreased around midday, indicating diurnal stomatal closure. Reduction in canopy conductance in the middle of the day was observed in all trees on a plot. Consequently, mean maximum canopy conductances per unit crown area per plot were lower in summer than in winter or autumn. Mean maximum canopy conductance was not related to maximum irradiance or to soil moisture content at depths above 0.35 m on any plot.

Thus, canopy transpiration rates in both eucalypt and rainforest canopy trees were dependent on (a) atmospheric humidity and available soil moisture below 0.35 m, and (b) canopy conductance to water vapour and water supply via roots and conducting tissues. Humidity of the air above the canopy is largely determined by the regional climate, and plays a dual role in driving canopy transpiration in these forests. Firstly, it determines the vapour gradient between the canopy and air in the mixed atmosphere, and secondly, it influences canopy conductance presumably through variation in leaf stomatal conductance in response to leaf to air vapour pressure difference.

Introduction

Sap flow is determined by both physical and physiological processes. As water transpires from a canopy, a gradient of water potential is formed between leaves and roots. Sap flow occurs in response to this potential gradient and is mediated by the liquid phase conductance (Boyer 1985; Whitehead 1985). Sap flow near the base of the trunk, however, may lag evaporation from the canopy due to the availability of stored water for transpiration. This storage effect, or capacitance (Landsberg *et al.* 1976; Whitehead and Jarvis 1981), is determined by both the amount of stored water and the water potential differential along the stem. In trees, both the capacitance and water potential gradient are influenced by wood anatomy (Tyree and Yang 1990), and consequently the lag between canopy transpiration and stem sap flow varies between species. When stored water contributes only small amounts to diurnal transpiration, sap flow responds quickly to a change in transpiration rate. Even with longer time lags, 24 hour total sap flow is equivalent to total daily transpiration if the change in total tree storage is zero. The heat pulse velocity technique may be readily used to measure sap flux. This technique has important advantages over direct and indirect methods of estimating canopy transpiration in large trees, because it integrates over the whole crown, does not require access to the canopy and, unlike micrometeorological

techniques which assume a uniform canopy, may be used in rough terrain, mixed plant communities and widely spaced trees (Denmead 1984).

The heat pulse velocity technique was used to measure sap velocity in mature rainforest and eucalypt trees in coastal southeastern New South Wales. In this region, vegetation distribution is strongly associated with slope and aspect (see Chapter 3). Earlier work (Yates, 1989; Barrett and Ash 1992) suggested that vegetation distribution may, in part, be determined by differences in plant responses between species to irradiance and moisture gradients associated with aspects. Given that microenvironment varies with aspect, it was hypothesised that *in situ* water use characteristics might differ between eucalypt and rainforest vegetation (Chapter 1). Thus, eucalypts might have attributes which would minimise water loss under high irradiance and low soil moisture. Conversely, rainforest species might maintain high rates of water use consistent with their occurrence in locations of higher soil moisture. Species differences in water use along gradients of light and water may be important in determining the differential distribution of vegetation in this region.

Three canopy tree species were chosen for this study. *Ceratopetalum apetalum* and *Doryphora sassafras* are dominant species of rainforests from sea level to 1000 m altitude at 28°S - 35.5°S and 28° - 36°S, respectively (Boland *et al.* 1984). Both species regenerate beneath the rainforest canopy and reach 35 m height (Floyd 1989). *Eucalyptus maculata* occurs from 25°S to 38°S (Boland *et al.* 1984) from sea-level to 400 m altitude (Austin 1978) and reaches 45 m height.

The aim of this field study was to determine relationships between water use and variation in irradiance, humidity and soil moisture in eucalypt forest and rainforest. This chapter describes (a) variation in regional climate and soil moisture content on each of two rainforest and eucalypt forest plots in a single catchment in southeastern New South Wales over a twelve month period (these plots were described in Chapter

3), (b) diurnal variation in sap flow, transpiration rate and canopy conductance in eight trees on each of these plots, in relation to variation in irradiance and saturation deficit, and (c) plot averaged variation in sap flow, canopy transpiration and conductance to water vapour in relation to average maximum irradiance, saturation deficit and plot averaged soil moisture content.

Methods

Climate and field site measurements.

Climatic measurements were made in an open pasture site (fetch at all azimuths > 300 m), 1 km inland from the Pacific Ocean between 24 May 1991 (Julian Day, J.D., = 144) and 22 May 1992, at the Edith and Joy London Foundation Australian National University research station at Kioloa (35° 32'S, 150° 22'E, altitude 10 m). The research station was located 5.2 km north of the field site described in Chapter 3. Temperature and relative humidity were recorded continuously on a thermohygrograph (Model 252-Ua, Wilh. Lambrecht, Gottingen, West Germany) within a Stevenson screen at 1.5 m height. The thermohygrograph was calibrated weekly against an aspirated psychrometer. Reliability of mechanical hair hygrometers may be affected by exposure to humidities above 90% and below 15% (Day 1985) and they have been criticised as being inaccurate for relative humidity measurements (Rundel and Jarrell 1989). However, by weekly calibration, drift in the relative humidity measurement was maintained below 10% of the measurement within a 7 day period. The water vapour saturation deficit, Δw, was calculated as,

$$\Delta w = \frac{(e_s - e_a)}{P} \qquad (5.1)$$

where e_s is the saturated vapour pressure at air temperature (Pa), P is the total air pressure (kPa) and e_a is the water vapour pressure of the atmosphere (Pa). The air pressure was determined from an automatic weather station (Ulladulla) at sea level, 26 km north of the field site. Maximum diurnal variation in P was 1.1% thus, within a 24-hour period P may be regarded as constant. Consequently, midday values of P were used, or measures within four hours of midday when these were not available. The vapour pressure at wet bulb temperature (Jones 1992; Day 1985) was determined from

$$e_a = h \,.\, e_s, \qquad (5.2)$$

where h is the relative humidity.

Weekly total rainfall was measured using a standard rain-gauge at 1 m height. Weekly total global irradiance on a horizontal surface was measured with a Rimco integrating pyranometer (Rimco, Burwood, Victoria).

In addition to continuous climate measurements, diurnal variation in irradiance and canopy microenvironment was quantified in conjunction with sap flux measurements. Diurnal variation in global irradiance incident on a horizontal surface was recorded at the research station, Kioloa, with an incident radiometer (Model CM-3, Kipp and Zonnen, Holland). Air temperature and wet bulb depression were measured using an aspirated psychrometer (Wilh. Lambrecht, Gottingen, West Germany) at various times throughout the day in clearings (approximately 30 m x 50 m) adjacent to access roads on ridges around the field site. Canopy temperature was recorded periodically throughout the day using an infra-red radiometer (Model 110, Everest Interscience Inc., California, USA.) in data averaging mode, calibrated to the Everest Calibration Source and a mercury thermometer. Mean plot canopy temperature was measured from beneath the canopy by pointing the radiometer at foliage clumps so as to exclude sky from the field of view, at elevation angles of between 40° and 50° in different azimuth

directions through 360°. The infra-red radiation received by the radiometer is potentially derived from three sources. These are (a) that portion of the sky included in the field of view, (b) the infra-red radiation reflected by the vegetation from the suroundings (eg. Wanjura and Upchurch 1991), and (c) the emitted radiation from the canopy. The error in canopy temperature due to inclusion of sky, calculated using the Stefan-Boltzmann law for a clear sky temperature of -40°C comprising 5% of the field of view and a canopy temperature of 20°C, would be 2°C. However, the potential error in the present study was minimised by measuring canopy temperature of foliage clumps, thereby excluding virtually all of the sky from the field of view.

Canopy temperature measurements were used to calculate mean plot canopy to air water vapour concentration difference (mole fraction) between 11:00 and 13:00 hours, vpd_C,

$$vpd_C = \frac{e_C - e_a}{P} \qquad (5.3)$$

where e_C is the average canopy leaf vapour pressure (Pa) which was assumed to be equivalent to the saturation pressure at the sites of evaporation within leaves (Farquhar and Raschke 1978) at average canopy temperature, and e_a is the partial pressure of water vapour (Pa) calculated from air and wet bulb temperature within the forest clearings (Day 1985; Jones 1992). Estimates of vapour pressure based on wet and dry bulb temperatures measured in forest clearings during early morning may not be representative of the humidity of the mixed air mass above the canopy. Such differences may be due to low wind speeds at that time of the day, resulting in inadequate mixing of air masses. Therefore, morning estimates of vpd_C have been disregarded. In the middle of the day wind gusts readily entered the clearings and mixing of air was considered sufficient such that relative humidities were assumed representative of the air mass above the canopy.

In conjunction with continuous climate measurements, soil moisture content, on a dry weight basis, was recorded weekly for 12 months at the field site. Samples of soil (between 0.3 and 0.8 kg) were collected using an 8 cm soil auger at two depths (0.15 and 0.35 m) from three randomly located points within each plot. The sampling depths were within the A-horizon which comprised a sandy-loam soil, overlying a sandy-clay clay layer at 0.4 - 0.5 m depth. Each sample was placed in a pre-weighed plastic oven bag and weighed before drying at 110^{o} C for 48 hours, then reweighed. Mean plot soil moisture content on a dry weight basis, above 0.35 m depth, was estimated from average gravimetric water content of the six samples from each plot.

Sap flow, canopy transpiration and conductance in rainforest and eucalypt forest trees.

Field studies on whole tree water use were conducted between July 1991 and March 1992, at the four field plots described in Chapter 3. Sap velocity was measured in eight trees on each plot using the heat pulse velocity technique described in Chapter 4. Three pairs of temperature sensors were inserted into the sapwood of each tree. Sensors were placed every 120^{o} around the stem at approximately 1.5 m above the ground. Measurements of heat pulse velocity were recorded every 15 minutes, over two clear days, for each tree. Sap velocities were calculated using equations 4.1 - 4.4 (Chapter 4), and sap flow was determined from the sap velocity weighted by the sapwood area associated with each sensor. Thus, diurnal sap flow was measured in 32 individual trees within a two week period in July/August and November/December 1991 and March 1992. Subsequently these measurement periods will be referred to as winter, summer and autumn, respectively.

Wood density and moisture fraction were determined from samples of sapwood taken using a 4 mm increment corer and placed immediately in a pre-weighed micro-Eppendorf tube. Prior sampling of four rainforest and eucalypt forest trees off-site,

indicated that within tree variation in moisture fraction was not greater than 6% of the mean. Consequently, excessive damage to trees, caused by repeated sampling, was avoided by removing one sample during each measurement period. Both sapwood density and moisture fraction at each measurement period were estimated using the techniques described in Chapter 4.

Total daily water use, Q_t, was determined from sap flow summed over a 24 hour period. Mean maximum sap flow, Q_c, was calculated from eight instantaneous measures of sap flow between 11:00 and 13:00 hours eastern standard time averaged over eight trees on each plot. Mean transpiration rate on a crown area basis, E_c, was calculated from mean sap flow and measured values of crown area for each tree (Table 3.2).

Average canopy conductance to water vapour per unit crown area, between 11:00 and 13:00 hours, was calculated as,

$$g_c = \frac{E_c}{vpd_c} \qquad (5.4)$$

and may be converted to mass flux density units by,

$$g' = g_c \frac{R\,T_a}{P} \qquad (5.5)$$

where g' is the canopy conductance per unit crown area in m s^{-1}, R is the gas constant (8.314 J mol^{-1} $^oK^{-1}$) and assuming that leaf temperatures are equivalent to air temperature (T_a in ^oK).

Analysis of variance, computed with Genstat-5 (Lane *et al.* 1987; Digby *et al.* 1989), was used to compare between plots at the different times of year for each measure of

water use. Since there was no effective replication of plots, the analysis of variance was based upon within plot to between plot variance. Extrapolation of results to other locations requires the assumption that plot choice was random within the forest. This assumption remains untested; however, plots appeared representative of the forest on a given aspect and, as such, it was considered that results may be extrapolated to the whole forest.

Results

Climate and field site microenvironment.

Daily maximum, minimum, and mean air temperature, as well as maximum saturation deficit are shown in Figure 5.1. Daily maximum air temperature over the 12 months between May 1991 and May 1992 ranged from 12° to 34° C, but with considerable day to day variation. However, the 10 day moving average varied seasonally between only 17° and 25° C. In contrast, minimum air temperature showed a stronger seasonal trend, with the 10 day moving average varying between 2° and 15° C. Daily minimum temperatures varied between -2° in winter and 22° C in summer. Lowest night-time temperatures were recorded from July to September 1991 (J.D. between 182 and 273), and corresponded to periods of clear night skies. Mean daily temperature varied between 6.5° and 28.0° C. Low mean daily temperatures occurred in late-winter 1991, following low night time minima. Consequently, the trend in 10 day mean temperatures varied between 10° and 20° C over the year.

Maximum daily saturation deficit varied between 0.1 and 33.3 Pa kPa^{-1}. Low saturation deficits were associated with rainfall events, whereas days with saturation deficits exceeding 20 Pa kPa^{-1} occurred in summer. The 10 day moving average remained between 9 and 13 Pa kPa^{-1} from spring until autumn. However, between May and July 1991 (J.D. between 144 and 182), average maximum saturation deficit

remained below 10 Pa kPa^{-1}. Saturation deficits measured in an open pasture at the research station, were compared with measurements taken in forest clearings at the field site (Fig. 5.2). At values less than 10 Pa kPa^{-1}, saturation deficits during summer measured at both sites over the whole day, were closely related. In winter and autumn, however, higher saturation deficits were observed at the research station than at the field site. At values greater than 10 Pa kPa^{-1}, particularly during summer, higher humidities were recorded at the research station than at the field site (Fig. 5.2).

There were two periods of relatively high rainfall between May 1991 and May 1992. These occurred between 31 May 1991 (J.D. = 151) and 19 July 1991 (J.D. = 200), and between 7 December 1991 (J.D. = 341) and 14 February 1992 (J.D. = 45; Fig. 5.3). Maximum weekly totals were 270 mm and 183 mm during winter and summer, respectively. A relatively dry period occurred between 20 July (J.D. = 201) and 6 December 1991 (J.D. = 340), in which the total rainfall did not exceed 105 mm. As a result, monthly totals between August and November, were below mean monthly precipitation for the region (Table 5.1). However, during June and July 1991 and between December 1991 and February 1992, total monthly rainfall exceeded monthly averages.

Weekly total global irradiance varied seasonally from 20.5 to 193.5 MJ m^{-2} $week^{-1}$ in mid-winter and mid-summer, respectively (Fig. 5.3). There was greater variability in weekly irradiance between December 1991 and April 1992, than during late winter-spring 1991. This variability was due to periods of greater cloud cover in summer/autumn than during late winter/spring.

Soil moisture content varied seasonally with rainfall, and differed between plots (Fig. 5.4). Peaks in each curve corresponded with preceding rainfall events. Soil moisture content declined on all plots between 20 July (J.D. = 201) and 6 December 1991 (J.D. =

340), in conjunction with the period of below average monthly rainfall and increasing weekly global irradiance (Fig. 5.3).

Mean soil moisture content was compared between plots for periods corresponding to sap flux measurements by an analysis of variance. These periods are indicated on Fig. 5.4. The plot x season term in the analysis of variance was significant ($P < 0.05$; Table 5.2). Mean soil moisture contents decreased significantly on all plots between winter and summer ($P < 0.05$; Fig 5.5). In winter, mean soil moisture content in the exposed aspect eucalypt forest plot was significantly lower than both sheltered aspect plots ($P < 0.05$), but not different from the gully bottom. In summer, the exposed aspect eucalypt forest plot was significantly lower than both rainforest plots ($P < 0.05$), but not different from the sheltered aspect eucalypt forest plot. There was a significant increase in soil moisture content between summer and autumn in all plots ($P < 0.05$) except in the exposed aspect eucalypt forest plot. During the autumn period soil moisture content on the sheltered aspect rainforest plot was greater than both the sheltered aspect eucalypt forest and gully bottom rainforest plots ($P < 0.05$), which in turn, were greater than the exposed aspect eucalypt forest plot ($P < 0.05$).

Observed soil profiles from pits dug on each plot, were similar on all plots. The upper horizons, to depths of between 40 and 80 cm, consisted of well drained sandy-loam soils containing very few coarse fragments. Below 50 cm, soils graded into sandy-clays, heavy-clays and saprolytic sandstones, characterised by lower water permeability.

Diurnal variation in sap flux, canopy transpiration and conductance in rainforest and eucalypt forest trees: Examples from six trees.

Sap flux was measured in 32 rainforest and eucalypt trees over each season. Diurnal variation in sap flux in response to diurnal variation in irradiance and humidity is

shown for two representative canopy trees of each species, one from each plot (Figures 5.6 - 5.8). These diurnal patterns of tree water use are considered individually to indicate how trees respond to diurnal variation in microclimate, and are representative of those obtained in other trees in the same plot, although smaller trees showed variation due to variable shading of their canopies. Such diurnal traces were then used to calculate mean values of canopy transpiration and canopy conductance described in later sections.

(a) Ceratopetalum apetalum, *gully bottom plot (Tree 20, Table 3.2).*

Maximum clear sky global irradiance (Fig. 5.6a) was 750 and 1250 J m^{-2} s^{-1} in winter and summer, respectively. An increase in cloud cover on the afternoon of 23 March 1992, decreased global irradiance from 1200 to below 750 J m^{-2} s^{-1}. Saturation deficit also increased after sunrise but lagged irradiance by up to 1.5 hours. Maximum daily saturation deficit occurred between midday and 14:00 hours on each day. Midday saturation deficit increased between winter and summer from 12 to 16 Pa kPa^{-1}.

Rainforest canopy to air temperature and vapour pressure difference both varied diurnally and between seasons (Fig. 5.6a). In winter, canopy temperature remained below air temperature throughout the day (maximum midday air temperature, T_{air} = 16.2°C). As a consequence the vapour pressure difference remained below saturation deficit. In contrast, canopy temperatures during summer increased to greater than 1°C above air temperature (T_{air} = 19.5°C) and vapour pressure increased to approximately 16 Pa kPa^{-1}. During autumn the maximum canopy to air temperature difference remained below zero during the day (T_{air} = 21.7°C) in conjunction with afternoon cloud.

Sap flow increased to a maximum 12 kg hr^{-1}, with increasing irradiance and saturation deficit in winter, early summer and autumn. In winter, maximum sap flow was

observed at midday in conjunction with maximum irradiance and saturation deficit. In summer, however, sap flow increased until approximately 9:00 - 9:30 hours and then remained relatively constant for the next 6 hours even though both irradiance and saturation deficit continued to increase.

Maximum canopy transpiration rates, on a crown area basis, ranged from 2 to 3 mmol m^{-2} s^{-1} from winter to summer, respectively. Canopy conductance to water vapour decreased to approximately 200 mmol m^{-2} s^{-1}, during the middle of the day in both winter and early summer.

(b) Ceratopetalum apetalum, *sheltered aspect plot (Tree 3, Table 3.2).*

Similar diurnal patterns of whole tree water use were observed in a tree of *C. apetalum* on the sheltered aspect (Fig. 5.6b). Maximum global irradiance during midday in summer and autumn reached values between 1300 and 1450 J m^{-2} s^{-1} possibly due to intense scattering of direct beam radiation by cumulus cloud in the clear sky (Gates 1980). Cloudy conditions on the morning of 21 November 1991, resulted in a reduction in global irradiance relative to clear sky conditions. Maximum saturation deficit recorded at around midday in each season was 10 Pa kPa^{-1}.

Canopy temperature remained below air temperature at midday in winter (T_{air} = 12.0°C), but peaked at 1°C above air temperature in conjunction with the intense peak in irradiance at midday in summer (T_{air} = 18.6°C). Autumn measurements were prevented by equipment malfunction. Canopy to air vapour pressure difference was equivalent to saturation deficit during summer, but remained below saturation deficit in winter and autumn since canopy temperatures were below air temperature (T_{air} = 22.8°C).

Maximum sap flow in winter occurred at approximately 14:00 hours in conjunction with maximum saturation deficit, rather than maximum irradiance. In summer, maximum sap flow occurred around midday, rather than earlier in the day as was observed in this species on gully bottom. This difference may be due to cloudy conditions on 21 November 1991, rather than any aspect related affects. A peak in sap flow was observed at around midday in summer coincident with the peak in irradiance. Maximum sap flow increased between winter and summer from 8 to 10 kg h^{-1}, respectively. Maximum sap flow in autumn was approximately the same as in summer. As a consequence, maximum canopy transpiration rate varied between 1.5 and 2.0 mmol m^{-2} s^{-1}. Canopy conductance to water vapour remained relatively constant throughout the middle of the day in winter, at around 200 mmol m^{-2} s^{-1}. In summer, however, canopy conductance declined throughout the day from approximately 250 mmol m^{-2} s^{-1} at 9:00 hours to less than 100 mmol m^{-2} s^{-1} at 17:00 hours.

(c) Doryphora sassafras, *gully bottom plot (Tree 28, Table 3.2).*

Figures 5.7a and 5.7b show diurnal variation in water use characteristics in one tree of *D. sassafras* on the exposed and sheltered aspect, respectively. In Fig. 5.7a, variable irradiance during the middle of the day in winter and summer, and during the morning in autumn, was due to the passage of cumulus clouds. Saturation deficits increased from 8 to 18 Pa kPa^{-1} between winter and autumn measurements. These higher values corresponded to incursion of relatively dry air of continental origin. Again canopy temperatures remained below air temperature in winter (T_{air} = 14.7°C) but were above air temperature during midday in summer (T_{air} = 28.2°C). During cloudy periods canopy and air temperatures were approximately equal. Canopy to air vapour pressure difference remained below 8 Pa kPa^{-1} in winter and autumn, and increased to 28 Pa kPa^{-1} at midday in summer.

Maximum midday sap flow coincided with maximum saturation deficits in winter. In all seasons nocturnal sap flow was observed. The rapid decline in sap flux at 1:30 hours in autumn was probably an artifact of the minimum measureable sap velocity (Chapter 4), rather than any sudden reduction in sap flow. Canopy transpiration rate was maintained at approximately 3 mmol m^{-2} s^{-1} in both winter and summer, but increased to 6 mmol m^{-2} s^{-1} in autumn. Canopy conductance to water vapour in winter, decreased during the middle of the day to approximately 500 mmol m^{-2} s^{-1}. However, during summer canopy conductance remained constant at approximately 200 mmol m^{-2} s^{-1} throughout the middle of the day. In conjunction with a vapour pressure difference of 4 Pa kPa^{-1} at midday in autumn, canopy conductance was estimated at 1450 mmol m^{-2} s^{-1} on a ground area basis. Although this value is apparently high, and may be an artifact of temperature measurement, an estimation of the average leaf conductance using plant area indices for the gully bottom plot (Fig. 3.9) yield a value of 350 mmol m^{-2} s^{-1}. This value is consistent with studies on individual leaves (eg. Korner and Cochrane 1985; Jane and Green 1985; Dye 1987; Dolman *et al.* 1991; Turner 1991).

(d) Doryphora sassafras, *sheltered aspect plot (Tree 10, Table 3.2).*

Water use characteristics of an individual tree of *D. sassafras* on the sheltered aspect were similar to those at the gully bottom (Fig. 5.7b). On each day, midday maximum saturation deficit was relatively constant between winter, summer and autumn, at approximately 11 Pa kPa^{-1}. Canopy temperature remained 0.5°C below and 0.5°C above air temperature at midday in winter (T_{air} = 14.6°C) and autumn (T_{air} = 28.6°C), respectively. In summer the canopy became up to 2°C cooler than air temperature (T_{air} = 22.8°C) throughout the afternoon. Maximum vapour pressure difference increased between winter and autumn, from 8 to a maximum of 18 Pa kPa^{-1}. Maximum sap flow remained constant between winter and summer, at around 10 kg h^{-1}, but increased in autumn to 12.5 kg h^{-1}. In summer sap flow remained relatively constant throughout the

middle of the day as global irradiance and saturation deficit increased. Maximum canopy transpiration rates varied between 2 and 3 mmol m^{-2} s^{-1} in winter/summer and autumn, respectively. Again nocturnal sap flow was observed, when saturation deficit was greater than 2 Pa kPa^{-1} during the night. Canopy conductance to water vapour remained constant between 9:00 and 14:00 hours in winter at approximately 250 mmol m^{-2} s^{-1}. In both summer and autumn a reduction in canopy conductance to approximately 200 mmol m^{-2} s^{-1} was observed during the middle of the day.

(e) Eucalyptus maculata, *exposed aspect plot (Tree 32, Table 3.2).*

Water use characteristics in an *E. maculata* on an exposed and sheltered aspect, are shown in Figures 5.8a and 5.8b. On the exposed aspect (Fig. 5.8a), saturation deficit was approximately 12Pa kPa^{-1} during measurement days in each season. In contrast to both rainforest species, the canopy temperature remained above air temperature (T_{air} = 14.2°C) in winter throughout the middle of the day. Conversely, canopy temperature remained below air temperature (T_{air} = 20.2°C) throughout the middle of the day in summer. Vapour pressure difference remained relatively constant between seasons at between 8 and 10 Pa kPa^{-1}. Sap flow peaked in winter in conjunction with peak irradiance but remained relatively constant between 10:00 and 15:00 hours in summer. Cloud in the morning of 25th March 1992, delayed the onset of sap flux until 8:00 hours. Maximum canopy transpiration rate remained between 1 and 2 mmol m^{-2} s^{-1} in each season. Canopy conductance to water vapour decreased from 400 to 150 mmol m^{-2} s^{-1} between 9:00 and 12:00 hours during winter. However, during summer, canopy conductance remained constant at approximately 150 mmol m^{-2} s^{-1}.

(f) Eucalyptus maculata, *sheltered aspect plot (Tree 15, Table 3.2).*

In a single *E. maculata* tree on the shaded aspect (Fig. 5.8b), midday canopy temperature was approximately equal to air temperature in winter (T_{air} = 14.6°C). In

summer, however, canopy temperature dropped below air temperature (T_{air} = 22.8°C) during the day. Again the vapour pressure difference remained relatively constant between seasons. Sap flow, and consequently canopy transpiration, remained relatively constant in summer between 10:00 and 15:00 hours. However, the transpiration rate on a crown area basis, was between 5-10 times that observed for this species on the exposed aspect. Canopy conductance decreased during the middle of the day in all seasons to a minimum of 400 and 600 mmol m^{-2} s^{-1} in both winter and summer/autumn, respectively.

Relationship between sap flow and environmental variables.

Sap flow responded differently to variation in irradiance and saturation deficit as shown in Figure 5.9. These data were derived from one tree of each species, measured during summer when maximum saturation deficit was <10 Pa kPa^{-1}. Saturation deficits were similar at both the research station and the field site (Fig. 5.2), thus, humidities measured at the research station were considered as representative of well mixed air above the forest canopy at this time. The data for *C. apetalum*, however, were influenced by cloud during the morning of 21 November 1991 (Fig. 5.6b), whereas data for both *D. sassafras* and *E. maculata* were collected on relatively clear days. The responses shown in Figure 5.9 are representative of other trees.

On each day saturation deficit increased with increasing global irradiance. However, for a given irradiance, saturation deficit was lower in the morning than during the afternoon because of differences in air temperature (Fig. 5.9 top row). This relationship was less pronounced for *C. apetalum* due to low morning irradiance. Sap flow also increased with increasing irradiance during the morning in both *D. sassafras* and *E. maculata*; however, a hysteresis in the response occurred with decreasing irradiance in the afternoon (Fig. 9 middle row). Sap flow remained high during the afternoon even though irradiance decreased.

Sap flow showed a closer relationship with changes in saturation deficit throughout the day (Fig. 9 bottom row). In both rainforest species, sap flow increased in the morning with increasing saturation deficit, and decreased in the afternoon as saturation deficit decreased along the same trajectory. At low saturation deficits, however, sap flow in *E. maculata* was lower in the afternoon than morning. Closer relationships between sap flow and humidity, than sap flow and irradiance, were consistantly observed in other trees of all species (data not presented).

Plot averaged variation in sap flow, transpiration rate and canopy conductance in rainforest and eucalypt forest trees.

(a) Maximum sap flow in relation to sapwood area.

Linear regression was used to examine the relationship between maximum sap flow and sapwood area per tree (Fig. 5.10) in order to determine whether relationships for eucalypt and rainforest trees were significantly different. Because of the nature of forest distribution in the catchment (Chapter 3), forest type and aspect were confounded. That is, rainforest was associated with the gully bottom and sheltered aspect, whereas eucalypt forest occurred on the exposed aspect and upper sheltered slopes. Consequently, data for each experimental plot were pooled as forest types. Furthermore, both *C. apetalum* and *D. sassafras* were grouped together into a "rainforest" category for this and subsequent analyses, since the range of all measured parameters overlapped for both these species.

The natural logarithm of maximum sap flow was linearly related to the natural logarithm of sapwood area ($r^2 = 0.396$, $p < 0.01$). This model was improved by fitting parallel regression lines separately through eucalypt forest and rainforest data (r^2 =

0.629, $p < 0.01$, Fig 5.10), but was not further improved by fitting different slopes or y-intercepts for each regression line. Additionally, incorporation of the 'season' term in the model did not significantly increase the variance explained by the model (r^2 = 0.626) and hence this term was excluded. Thus, maximum sap flow in any tree was, in part, dependent on sapwood area, and for a given maximum sap flow, sapwood area in eucalypt trees was lower than in rainforest trees.

(b) Sap flow and canopy transpiration.

Analysis of variance was used to compare within plot to between plot variation in mean water use parameters for all trees (Table 5.2). There were no significant differences in mean daily sap flow integrated over 24 hours, between plots (Table 5.2). These averages were based on sap flow in eight trees per plot, which differed in size. Mean total sap flow, Q_t, was significantly lower in winter than in either early summer or autumn ($p < 0.05$), with Q_t = 60.4, 82.9 and 78.3 kg d^{-1} for winter, summer and autumn, respectively.

Plot, season and plot x season terms were not significant in the analysis of variance of mean sap flow between 11:00 and 13:00 hours, Q_c, suggesting that variation in mean maximum sap flow within a plot was greater than variation in maximum sap flow between plots (Table 2). This was because the range of tree size within each plot overlapped between plots.

The analysis of variance of mean maximum canopy transpiration rate, E_c, did produce a significant plot x season interaction term ($P<0.05$; Table 5.2). Mean transpiration rates were 3.6 mmol m^{-2} s^{-1} in winter and 3.2 mmol m^{-2} s^{-1} in autumn in the gully bottom rainforest plot ($P<0.05$; Fig. 5.11a). In contrast, mean transpiration rates in the exposed aspect eucalypt forest plot were 2.1 mmol m^{-2} s^{-1} in winter and 1.6 mmol m^{-2} s^{-1} in autumn. In sheltered aspect plots, mean transpiration rates were 1.7 and 3.1

mmol m^{-2} s^{-1} in winter and autumn in eucalypt forest, and 1.7 and 2.5 mmol m^{-2} s^{-1} in winter and autumn in rainforest. Summer values for transpiration were between winter and autumn values on all plots.

(c) Canopy conductance to water vapour.

There were significant plot, season and plot x season terms for the analysis of mean midday canopy conductance to water vapour (Table 2). Canopy conductance on the gully bottom was greater than all other plots in winter, 1991 and autumn, 1992 ($P<0.01$; Fig. 5.11b) but not in summer. At this plot, canopy conductance decreased from 600 to 220 mmol m^{-2} s^{-1} between winter and early summer 1991, and then recovered by autumn 1992 to 600 mmol m^{-2} s^{-1}. Higher canopy conductances in winter and autumn on the gully bottom rainforest plot, occurred in association with surface saturation of the soil as indicated by running water in the creek adjacent to this plot. This was confirmed by soil cores taken shortly after sap flux measurements (20 August 1991), which indicated a sub-surface saturated zone at 1.45 m. A dry creek during summer, however, was associated with lower canopy conductance in rainforest at the gully bottom, with values similar to other plots. The strong seasonal effect in canopy conductance (variance ratio 22.20, Table 2) was also observed in the exposed aspect eucalypt plot, where canopy conductance was higher in autumn than in summer ($P<0.05$). Maximum canopy conductances in mass flux density units were 1.41 and 1.42 cm s^{-1} at the gully bottom rainforest plot during winter and autumn periods, and on other plots between 0.43 and 0.85 cm s^{-1}, throughout the year.

(d) Relationship between maximum canopy conductance and environmental variables.

Relationships between microenvironment and mean maximum canopy conductances at the whole plant level are shown in Fig. 5.12. At the highest midday global irradiances

during summer, mean canopy conductance on all plots was lower than during midday in winter and autumn (Fig. 5.12a). Additionally, mean canopy conductance was linearly related to midday saturation saturation deficits measured in forest clearings, when data from the gully bottom rainforest plot during winter and autumn were excluded (Fig 5.12b). Mean plot midday canopy conductance decreased with increasing saturation deficit (solid line Fig. 5.12b; $r^2 = 0.58$; $P < 0.05$). No relationship, however, was evident between canopy conductance and soil moisture content at depths above 0.35 m on all plots (Fig. 5.12c). These data indicate that, apart from the gully bottom plot, there were no apparent plot differences in mean midday canopy conductance to water vapour between plots and that canopy conductance decreased with increasing saturation deficits.

Discussion

Climate and field site microenvironment.

The climate of coastal southeastern New South Wales, Australia, is influenced predominantly by a maritime air stream and is characterised by relatively high humidities and annual precipitation above 1000 mm (Kalma and McAlpine 1978). However, incursion of relatively dry air of continental origin, generally associated with the easterly passage of high pressure systems, is common during summer (Austin and Yapp 1978). This region usually experiences lower monthly precipitation and more rainless days between July and September, due to the influence of low pressure systems at high latitudes on the prevailing winds. These systems produce a predominantly westerly air stream, resulting in orographic uplift of air and consequently higher rainfall on the western slopes of the Great Dividing Range (Austin and Yapp 1978). As a result, relatively dry air descends onto the coastal plain during late winter. During summer,

however, monthly rainfall is higher because of the prevailing moist onshore winds (Kalma and McAlpine 1978).

The meteorological data collected in an open field at Kioloa between May 1991 and May 1992, corresponded to the general trends outlined above. Rainfall was slightly greater than the annual average (Table 5.1) with the distribution biased towards early winter and summer (Fig. 5.3). An association between summer rainfall patterns and rainforest distribution throughout eastern Australia has been reported (Webb and Tracey 1981) consequently, the frequency of rainfall events in summer may be crucial to the survival of rainforest species in both southeastern New South Wales (Helman 1983) and further north in Queensland (Doley *et al.* 1987). Maximum saturation deficits were more frequent and more extreme during the summer period. The lowest minimum temperatures occurred on clear nights during late winter and early spring, with freezing temperatures recorded on nine occasions (Fig. 5.1). Read and Hill (1989) showed that *C. apetalum* and *D. sassafras* were the least frost resistant of 8 temperate rainforest species from southeastern Australia, and suggested that increased frost incidence at higher latitudes may restrict the latitudinal distribution of both these species.

Average maximum daily temperature, derived from a 10-day moving average, varied between 17° and 25°C in winter and summer, respectively. Hill *et al.* (1988) showed that maximum rates of photosynthesis in *C. apetalum* and *D. sassafras* occurred at approximately 25°C and between 22° and 25°C, respectively. Only 12 of the 130 days between 24th May 1991 (J.D. = 144) and 30th September 1991 (J.D. = 273), had maximum temperatures greater than or equal to 22°C. Thus, cooler temperatures during winter in this region, may be sub-optimal for photosynthesis and possibly growth in both these rainforest species. Pook (1984a) suggested that growth in *E. maculata* stopped when mean daily temperature was less than 10°C, which occurred on 26 days between May 1991 and May 1992 (Fig. 5.1).

Mean global irradiance varied seasonally as solar elevation changed (Fig. 5.3). Lowest values were recorded during winter due to low solar elevation, however, greater variation in the data recorded during summer was attributed to increased cloud cover.

Soil moisture contents at any location are determined by the sum of water inputs and outputs (Fig. 5.13). Water inputs in the unsaturated layer are primarily by precipitation, less canopy interception, and drainage from upslope soil. Water outputs include: (a) lateral drainage, which is determined by soil properties and slope angle (Moore *et al.* 1986; O'Loughlin 1986; Moore *et al.* 1988), (b) deep drainage into the water table, (c) vegetation transpiration, and (d) soil evaporation, determined partly by surface irradiance. Mean soil moisture content above 0.35 m at the field site, varied throughout the year in all plots (Fig. 5.4 and 5.5). Mean soil moisture content on the exposed aspect eucalypt plot was always lower than other plots. Soil moisture contents between other plots, however, were not significantly different in winter and summer. Lower soil moisture contents in the exposed aspect eucalypt forest plot, may be due to higher soil evaporation rates, soil drainage and transpiration by the grass and shrub understorey. Higher soil evaporation rates on exposed aspects may be due to relatively high irradiances, producing high ground surface temperatures (Chapter 1). Low plant area indices in eucalypt forest (Chapter 3) result in relatively high ground surface irradiance on exposed aspects, due to low radiation interception by the canopy (Turton and Duff 1992). Higher plant area indices in rainforest, reduce the influence of direct beam irradiance on soil temperatures and soil evaporation rates, and may contribute to higher mean soil moisture contents on these plots at depths < 0.35 m, despite greater rainfall interception by the canopy.

Diurnal sap flow, canopy transpiration and conductance in rainforest and eucalypt forest trees.

The heat pulse velocity technique is a convenient means of measuring whole tree water use which, when tree storage effects are small, may be directly related to transpiration from the canopy. Recent reports indicate good agreement between this technique and transpiration rates estimated from simultaneous energy balance measurements (Granier 1987; Ham *et al.* 1990; Granier *et al.* 1990; Hatton and Vertessy 1990; Granier *et al.* 1992; Cienciala *et al.* 1992). In the present study the rapid response by sap flow at the stem base to diurnal variation in microclimate after sunrise, suggested that the majority of water used in transpiration was met by direct uptake. The time lag between increased irradiance at sunrise and an increase in sap flow, did not exceed 0.5 to 1 hour (Figures 5.6 - 5.8). It was assumed, therefore, that variation in sap flow at the stem base, was closely related to variation in transpiration from the canopy. These values were similar to time lags observed in *Salix fragilis* (Cermak *et al.* 1984), *Pseudotsuga menziesii* and *Pinus ponderosa* (Lopushinsky 1986), *Picea abies* (Werk *et al.* 1988), 9 m tall *Eucalyptus regnans* (Dunn and Connor 1991) and *Nothofagus fusca* and *N. menziesii* (Kostner *et al.* 1992). Longer lag times between reduction in both irradiance and sap flow in the afternoon, of 1.5 hours in *P. radiata* (Hatton and Vertessy 1990), 3 hours in *Larix* and *Picea* species (Schulze *et al.* 1985) and 2 hours in *Pinus pinaster* (Diawara *et al.* 1991), were attributed to recharge of stem water storage and equilibration of the stem-canopy water potential gradient formed during the day. However, in all of the above studies, midday sap flow approximated transpiration rate.

(a) Conductance to water vapour in forest canopies.

Leaf conductance is defined as the ratio of evaporation rate per unit leaf area to humidity differential across the leaf surface (Cowan 1977). A similar relationship may be used to describe water vapour transfer from a forest canopy (Monteith 1981).

However, the canopy conductance term is more complex. The total pathway conductance to water vapour, g_c, is determined by the parallel sum of stomatal and leaf boundary layer conductances, and the series sum of leaf and canopy boundary layer conductances.

$$\frac{1}{g_c} = \frac{1}{g_{surface}} + \frac{1}{g_a} \qquad (5.6)$$

where g_a is the boundary layer conductance of the forest canopy and $g_{surface}$ is the total stomatal conductance of all leaves per unit ground area (Jarvis and McNaughton 1986). Earlier work assumed that canopy surface conductance could be derived from the parallel sum of leaf conductances (Jarvis 1981). However, this relationship holds only where canopies are well ventilated and vertical humidity and temperature gradients are absent (Jarvis and McNaughton 1986). Other reports suggested that total stomatal conductance and the sum of leaf conductances are not necessarily equal (Stewart and Thom 1973; Finnigan and Raupach 1987; Baldocchi *et al.* 1987; Baldocchi 1989). The surface conductance of a forest also depends on radiation transfer and boundary layer conductances within the canopy (Baldocchi *et al.* 1991) as well as stomatal responses to vertical gradients of temperature and humidity (Jarvis and McNaughton 1986). If the boundary layer conductance is large, which is usually the case in forests (Monteith 1981), then the total pathway conductance becomes approximately equal to the total stomatal conductance of the canopy. When g_a is large the term $\frac{1}{g_a}$ becomes small and hence g_c is approximately equal to $g_{surface}$. Thus, in the discussion below, variation in canopy conductance (g_c in equation 5.4 and 5.6) is assumed to be closely related to variation in total stomatal conductance ($g_{surface}$) of the canopy.

Apart from errors associated with using infra-red radiation to measure leaf temperatures of forest canopies (outlined in the Methods), further error in the measurement of canopy conductance may occur if average canopy temperatures were not representative of the

temperatures of leaves contributing most to water loss by the canopy. Both Dunin *et al.* (1989) and Huband and Monteith (1986) reported discrepancies in estimated transpiration rates from crop canopies using canopy temperature measurements derived from infra-red radiometry. However, Smith *et al.* (1988) found good agreement between stomatal resistance estimated from infra-red canopy temperature measurements and porometry. In the present study, canopy temperatures measured by infra-red radiometry were assumed to be equivalent to the temperature of leaves that are the major source for water vapour in the canopy in rainforest and eucalypt plots. This assumption probably holds in well ventilated canopies at high boundary layer conductances where significant gradients of humidity and temperature do not develop within the canopy (Jarvis and McNaughton 1986). For example, Aston (1985) found a temperature differential between upper and lower canopy leaves (leaf area index = 4.3) of <3^{o}C in regenerating *E. maculata* forest during spring 1983.

A further source of error in the estimation of canopy conductance in this study may occur if humidities measured in forest clearings were not representative of the well mixed air above the canopy. For example, a 2^{o}C error in the measurement of air temperature at 20^{o}C with a wet bulb depression of 5^{o}C, would produce a 12% error in vapour pressure difference in equation 5.3. Previous reports have shown that, in forests, the evaporative demand of air in the mixed layer, was readily imposed on the forest understorey by wind gusts (Denmead and Bradley 1985; Black and Kelliher 1989; Kelliher *et al.* 1990). Consequently, in a clearing of width larger than canopy height, located adjacent to access roads on ridge tops, it was assumed that humidity measurements were indicative of air above the canopy. Comparisons of humidity measurements between forest clearings and an open pasture 5.2 km distance (Fig. 5.2), showed differences between these two sites. At large saturation deficits, drier conditions were observed at the forest site than in open pasture, with the converse occurring at lower saturation deficits, particularly in autumn. Pearce *et al.* (1980) also reported lower saturation deficits over forest than over pasture at high humidity after

rainfall, but the difference was not signficant when the canopy had dried. The difference in saturation deficit between forest and pasture in the present work, may be due to differences in transpiration rate and boundary layer conductance between grassland and forest (McNaughton and Jarvis 1983), in addition to topographic effects associated with each site.

In this study, estimates of canopy conductance per unit crown area, apart from one value of 1450 mmol m^{-2} s^{-1} in *D. sassafras*, are up to 1000 mmol m^{-2} s^{-1}. Wong and Dunin (1987) reported canopy conductances within a whole tree enclosure of less than 1000 mmol m^{-2} s^{-1}, on a ground area basis, in *E. maculata*at the Kioloa State Forest. Both Cienciala *et al.* (1992) and Granier *et al.* (1992) reported conductances below 800 mmol m^{-2} s^{-1} on a ground area basis, from measurements of sap flow in *Pinus sylvestris* and two tropical species of South America (*Simarouba amara* and *Goupia labra*), respectively. Thus, values of canopy conductance measured using the techniques in this study, are comparable with other forests.

(b) Diurnal canopy transpiration and conductance in rainforest and eucalypt forest trees.

Diurnal variation in sap flow in all trees (Figures 5.6 - 5.8) may be explained by both canopy stomatal responses to environment and the direct influence of humidity on evaporative demand. Sap flow varied diurnally in all trees, apparently in response to variation in both irradiance and saturation deficit. In general, a four phase response was observed. Firstly, sap flow increased rapidly in the morning, in conjunction with increasing irradiance and saturation deficit. The second phase was characterised by constant sap flow during the middle of the day, as both irradiance and saturation deficit continued to increase. In the third phase, sap flow decreased during the afternoon in association with decreasing saturation deficit. Finally, nocturnal sap flow decreased to minimum values unless relatively large saturation deficits occurred at night.

A rapid increase in sap flow during the early morning was consistent with stomatal opening in response to light, and high conductances to water vapour at low leaf to air vapour pressure differences. The influence of increasing atmospheric saturation deficit on transpiration rates during the morning is, however, confounded with increasing irradiance, because incoming radiant energy increases air temperature and consequently, its saturation vapour pressure (Jarvis 1981). At high humidities and at low boundary layer conductances after sunrise, transpiration may respond directly to increasing irradiance. As saturation deficit increases during the morning, and where canopy temperatures are close to air temperature, transpiration rate becomes more coupled to the saturation deficit and less dependant on irradiance (McNaughton and Black 1973; McNaughton and Jarvis 1983; Verma *et al* 1986; Jarvis and McNaughton 1986; Finnigan and Raupach 1987). The results presented in Figure 5.9 support the coupling of diurnal canopy transpiration in both rainforest and eucalypt forest, to humidity during the middle of the day and throughout the afternoon. Thus, both irradiance and saturation deficit determine transpiration from the canopy, but the relative importance of each term varies during the day (Price and Black 1991; Kostner *et al.* 1992).

The second phase in diurnal sap flux, is characterised by the maintenance of constant sap flux as both irradiance and saturation deficit increase. This phase represents possible control of canopy transpiration by stomatal restriction of water loss. As saturation deficit increased, canopy conductance to water vapour decreased, suggesting stomatal closure (Figures 5.6 - 5.8), thereby reducing water loss. However, the relationship between transpiration rate, conductance and the vapour pressure gradient is complicated by the influence of conductance on the vapour gradient in equation 5.4 and *vice versa.* Stomatal conductance in many species is inversely related to the vapour pressure difference between the atmosphere and both leaves (Landsberg and Butler 1980; Warrit *et al.* 1980; Schulze and Hall 1982; Kaufmann 1982; Grantz 1990;

Nonami *et al.* 1990; Aphalo and Jarvis 1991; Kappen and Haeger 1991; Turner 1991) and the canopy (Jarvis 1981; McNaughton and Jarvis 1983; Stewart and de Bruin 1985; Munro 1989; Baldocchi *et al* 1991). That is, stomata tend to close as humidity decreases. However, variation in stomatal conductance itself may influence the vapour pressure gradient by altering leaf energy balance (Cowan 1968 and 1988). Thus, stomatal responses to humidity may themselves alter the leaf to air humidity difference.

The interaction between stomatal function, humidity gradients and transpiration rate are processes which determine leaf and canopy energy balance, and may explain observed trends in canopy to air temperature differences in each forest type (Figures 5.6 - 5.8). In general, canopy to air temperature and vapour pressure differences were higher in both rainforest species, in summer than in winter or autumn. This may have been due to stomatal closure in response to lower humidity during summer, thereby restricting potential water loss, and hence latent heat loss. A reduction in latent heat loss from leaves in the canopy may have contributed to higher canopy temperatures. In eucalypts, however, steeper leaf inclination (Anderson 1981) may have reduced intercepted irradiance in summer, contributing to lower canopy temperatures at that time.

Diurnal variation in sap flow as reported in this study, is consistent with published reports on many species. Ladefoged (1963), using the heat pulse velocity technique, suggested that transpiration in various species of a Norwegian *Fagus-Quercus* forest generally increased in the morning in response to increased irradiance, however maximum sap flow was dependant on relative humidity. Subsequent work in *Eucalyptus marginata* (Doley and Grieve 1966; Doley 1967), *Larix* and *Picea* species (Schulze *et al.* 1985), *Pseudostuga menziesii* (Cohen *et al.* 1985; Lassoie *et al.* 1977), *Picea abies* (Werk *et al.* 1988), *Pinus ponderosa* (Lopushinsky 1986), *Nothofagus solandri* (Swanson *et al.* 1979) and *Quercus velutina* and *Q. alba* (Miller *et al.* 1980) have shown that increased sap flow after sunrise, occurred in response to a rapid

increase in stomatal conductance. Stomatal conductance then decreased in late morning and throughout the afternoon.

Midday reduction in stomatal conductance has also been reported in many other species. In eucalypts, stomatal conductance has been observed to decrease in response to increasing saturation deficits at midday (Korner and Cochrane 1985; Pereira *et al.* 1986; Kuppers *et al.* 1987; Wong and Dunin 1987). Similar responses have been observed in rainforest species in Australia (Pearcy 1987; Doley *et al.* 1987; Unwin and Kriedemann 1990), Amazonia (Dolman *et al.* 1991), China (De Lillis and Sun 1990) and New Zealand (Jane and Green 1985), and in conifers (Granier *et al.* 1990) and five central European woody hedge-row species (Kuppers 1984). Thus, stomatal closure during the middle of the day at high saturation deficits, appears to be a common mechanism controlling water loss in a diverse range of plant communities (Tenhunen *et al.* 1987).

Sap flux was observed at night in both rainforest and eucalypt species (Figures 5.6 - 5.8). Observations of nocturnal sap flux and the maintenance of relatively high stomatal conductance at night, have been made in apple and kiwifruit at $\Delta w > 1.0$ Pa kPa^{-1} (Green *et al.* 1989), and in *Pinus ponderosa* and *Pseudotsuga menziesii,* (Lopushinsky 1986). Kuppers (1984) also found partially open stomata during darkness in five hedge row species of central Europe. Sap flow during this phase may be a consequence of both continuing transpiration from the canopy and recharge of water stored in the trunk and branches which had contributed to transpiration during the day.

Similar patterns of diurnal sap flow were observed in both rainforest and eucalypt canopy trees in the catchment in southeastern New South Wales. The relationship between transpiration rate, humidity and stomatal control of water loss is comparable to previous studies suggesting a strong couping between canopy and atmosphere. The strong coupling is attributed to high boundary layer conductances of the forest which

contribute to similar canopy and air temperatures. Canopy transpiration was less dependant on irradiance than on canopy to air vapour pressure difference. However, increased vapour pressure gradient during summer on rainforest plots relative to eucalypt plots, was partly attributed to greater intercepted radiation by the rainforest canopy, in conjunction with decreased latent heat loss.

Plot averaged variation in sap flow, canopy transpiration and conductance in rainforest and eucalypt forest trees.

(a) Mean maximum and total daily sap flow.

Transpiration is dependent on the evaporative demand of the environment and on the capacity of the plant to supply water to the leaves. Thus, a relationship between sapwood area and maximum sap flow may be expected. Indeed, ln(sapwood area) was linearly related to ln(maximum sap flow). This relationship, however, was different between rainforest and eucalypt forest trees, but independent of plot (Fig. 5.10). For a given maximum sap flow, a lower sapwood area was observed in eucalypt forest trees, than in rainforest trees. This may imply a lower internal resistence to water transport (Zimmermann 1983) in eucalypts, which may be advantageous on relatively dry sites (eg. Tyree *et al.* 1991) such as exposed aspects and ridge tops.

Mean maximum sap flow averaged over eight trees on each plot, was not dependent on forest type or season (Table 5.2) despite differences in mean crown area (Fig. 3.10) and plant area index (Fig. 3.9). However, sap flow integrated over 24 hours was significantly lower in winter, than in summer or autumn. Because maximum sap flow was not different between seasons, greater total water use in summer occurred because of longer daytime periods at maximum flow, rather than intrinsically higher sap flow.

(b) Mean maximum canopy transpiration.

Mean canopy transpiration rate, measured between 11:00 and 13:00 hours, did not vary significantly between seasons in either the gully bottom rainforest or exposed aspect eucalypt plots (Fig. 5.11a). On both sheltered aspect plots, however, canopy transpiration was higher in autumn 1992 (rainforest = 2.5 mmol m^{-2} s^{-1}, eucalypt forest = 3.1 mmol m^{-2} s^{-1}), than in winter 1991 (rainforest and eucalypt forest = 1.7 mmol m^{-2} s^{-1}). The maximum transpiration rates, on the sheltered aspect, are equivalent to values of 4.8 and 3.9 mm d^{-1} in rainforest and eucalypt forest in autumn, and 2.7 mm d^{-1} in both forest types in winter, when expressed in mass flux density units. Dunin *et al.* (1985) reported evapotranspiration rates from a lysimeter, in a 10 year old regenerating stand of *E. maculata* in the adjacent Kioloa State Forest, for one day each in May and September 1980 and April 1981. Maximum rates between 11:00 and 13:00 hours were from 2.5 to 3.0 and 3.5 to 4.2 mm d^{-1} for each day in May and September 1980, respectively. However, rates between 11:00 and 13:00 hours on a single day in April 1981 were between 8.5 and 11.0 mm d^{-1} (Dunin *et al.* 1985). These higher rates are equivalent to evapotranspiration rates in molar units of 5.5 and 7.1 mmol m^{-2} s^{-1}, respectively. Somewhat higher rates of evapotranspiration may be expected from the lysimeter, than those measured by the heat pulse velocity technique, as lysimeter measurements include not only transpiration from the eucalypt canopy, but also that from the understorey shrubs and grasses, as well as soil evaporation. The heat pulse velocity technique, however, estimates transpiration from only the overstorey component.

(c) Mean maximum canopy conductance to water vapour.

Canopy conductance to water vapour per unit crown area, averaged over eight trees per plot between 11:00 and 13:00 hours, was greater in the gully bottom rainforest plot in winter and autumn, than in all other plots (Fig. 5.11b). Canopy conductance showed no

relationship with mean maximum irradiance (Fig. 5.12a) presumably because the leaves contributing most to canopy transpiration, which occur on the outside of the canopy (eg. Cermak *et al.* 1984; Doley *et al.* 1987 and 1988; Dolman *et al.* 1991; Petersen *et al.* 1992), are light saturated during the middle of the day in all seasons. Additionally, no relationship was observed between mean soil moisture content at depths <0.35 m and canopy conductance (Fig. 5.12c), presumably because water supply for transpiration is derived from deeper in the soil profile (eg. Doley 1967; Greenwood and Beresford 1979; Cermak *et al.* 1980; Whitehead and Jarvis 1981; Carbon *et al.* 1981; Chaney 1981).

By assuming that leaf area index was approximately equal to plant area index (Chapter 3), the "average leaf" response to saturation deficit was determined from the ratio of canopy conductance to plant area index (Whitehead *et al.* 1984; Fig. 5.14). The relationship between average leaf conductance and saturation deficit were similar irrespective of forest type or topographic position. This decrease in leaf conductance with increasing saturation deficit was consitent with field studies on whole trees or forest canopies (eg. Whitehead *et al.* 1984; Stewart and de Bruin 1985; Munro 1989; Cienciala *et al.* 1992; Granier *et al.* 1992; Kostner *et al.* 1992) and individual leaves (eg. Myers and Neales 1984; Korner and Cochrane 1985; Doley *et al.* 1987; Dye 1987). The similarity in the average leaf conductance/saturation deficit response between rainforest and eucalypt forest plots may be due to the strong coupling between the forest canopy and atmosphere at the stand scale (Jarvis 1986), even though at the leaf scale individual leaves may be responding to the environment in their immediate vicinity.

Influence of aspect on transpiration in rainforests and eucalypt forests of southeastern New South Wales.

The second and third hypotheses in Chapter 1, proposed that differences in canopy structure between rainforest and eucalypt forest would be manifest as differences in water use characteristics between forest types on different aspects. Eucalypt species would display conservative water use characteristics which may be advantageous on exposed aspects and ridge tops, where soil moisture contents may be lower than at the gully bottom and on sheltered aspects. Conversely, rainforest species were expected to possess less conservative water use characteristics consistent with occurence on presumably moister sites. The results from the present study partly conform to the hypotheses outlined above. Higher transpiration rates in the gully bottom rainforest plot in winter and autumn (Fig. 5.11a) may be due to both greater water availability and higher leaf area index resulting in greater canopy conductance per unit crown area. Whereas higher transpiration rates in summer, may have been due to both a higher leaf area index and a greater canopy to air vapour presure difference, due to increased light interception by more horizontally orientated leaves. However, on slopes above the gully bottom, no apparent differences in water use characteristics between rainforest and eucalypt forest plots were observed. This result was not consistent with hypotheses proposed in Chapter 1, although, a lower sapwood area per unit maximum sap flux in eucalypts may imply a lower internal resistance to water transport, an attribute which may be advantageous for obtaining water from depth in the soil such as on exposed aspects and ridge tops.

The relationships between conductance and humidity (Figs. 5.12b and 5.13) do indicate a strong coupling between canopy and atmosphere as defined by McNaughton and Jarvis (1983 and 1991; Jarvis and McNaughton 1986). They re-expressed the Penman-Monteith equation as,

$$E = \Omega E' + (1-\Omega) E'' \qquad (5.7)$$

where E' is the equilibrium evaporation rate given by,

$$E' = \frac{\varepsilon (R_n - S)}{\lambda (\varepsilon + 1)} \qquad (5.8)$$

where R_n is the net radiation (J m^{-2} s^{-1}) and S is the energy stored in biomass, the air mass and the soil. E'' is the imposed evaporation rate,

$$E'' = \frac{C_p \Delta w P g_{surface}}{\lambda \gamma} \qquad (5.9)$$

where C_p is the molar heat capacity of dry air (29.3 J mol^{-1} $^oK^{-1}$), γ is the psychrometric constant (66.1 Pa $^oK^{-1}$ @ 20^{o}C) and λ is the molar latent heat of vaporisation of water (44 kJ mol^{-1}). The coupling coefficient, Ω, is derived as,

$$\Omega = \frac{\varepsilon + 1}{\varepsilon + 1 + \left(\frac{g_a}{g_{surface}} \right)} \qquad (5.10)$$

where ε is the slope of the saturation deficit curve in molar units and g_a is the canopy boundary layer conductance (mol m^{-2} s^{-1}). The coupling coefficient in equation (5.10), is inversely related to the ratio of the boundary layer to canopy conductance. Thus, Ω is low in forest canopies (McNaughton and Jarvis 1983; Whitehead *et al.* 1984) and equation 5.7 then predicts that canopy transpiration is strongly dominated by atmospheric humidity and canopy conductance, and much less influenced by intercepted radiation. However, stomata respond to both humidity and soil moisture (Schulze and Hall 1982; Schulze 1986), consequently, the surface conductance term in equation 5.9 may itself be partly dependent on the saturation deficit term in the same equation. That is, the transpiration rate may remain constant even though humidity may

vary, because stomata respond to humidty. Thus, transpiration rates in forest canopies tend to be independent of forest species composition and restricted within a narrow range (Roberts 1983). In the present study, forest transpiration rates were determined by both physical processes, determining plant water availability and the evaporative demand of the atmosphere, and biological processes, determining the conductance of water vapour from the canopy and supply of water via roots and stems, to the canopy.

Canopy transpiration rates in temperate rainforests and eucalypt forests of eastern Australia are therefore more dependent on regional variation in atmospheric humidity, on stomatal responses to humidity and on seasonal variation in sub-surface water availability, than on aspect mediated variation in microenvironment near the ground surface. Thus, the differential distribution of rainforest and eucalypt forest species with aspect may be determined more by processes controlling plant growth and establishment at the seedling and sapling scale, rather than processes controlling established tree growth and water use at the forest scale.

Table 5.1.
Monthly total precipitation for Kioloa research station during the period 24 May 1991 to 22 May 1992 and mean monthly precipitation for Batemans Bay, 17 km south of the field site between 1911-1970 (collated by Kalma and McAlpine 1978).

Month	Kioloa (mm)	Batemans Bay (mm)
June	335	100
July	170	70
August	5	51
September	47	64
October	29	77
November	21	83
December	149	91
January	138	100
February	241	95
March	43	105
April	77	103
May	0	112
Total	1255	1051

Table 5.2.
Summary table of the analysis of variance showing degrees of freedom (d.f.), variance ratios and their significance for all plot, season and plot x season effects on mean soil moisture content (SMC), total daily sap flux (Q_t), mean maximum sap flux (Q_c), mean maximum canopy transpiration rate (E_c) and mean canopy conductance to water vapour (g_c). * significant $P < 0.05$; ** significant $P < 0.01$.

Source	d.f.	SMC	d.f.	Q_t	Q_c	E_c	g_c
plot	3,12	23.81**	3,26	2.66	2.41	2.03	3.36*
season	2,12	73.13**	2,52	6.39**	1.81	1.01	22.20**
plot x season	6,12	4.22*	6,52	2.12	0.70	2.32*	4.49**

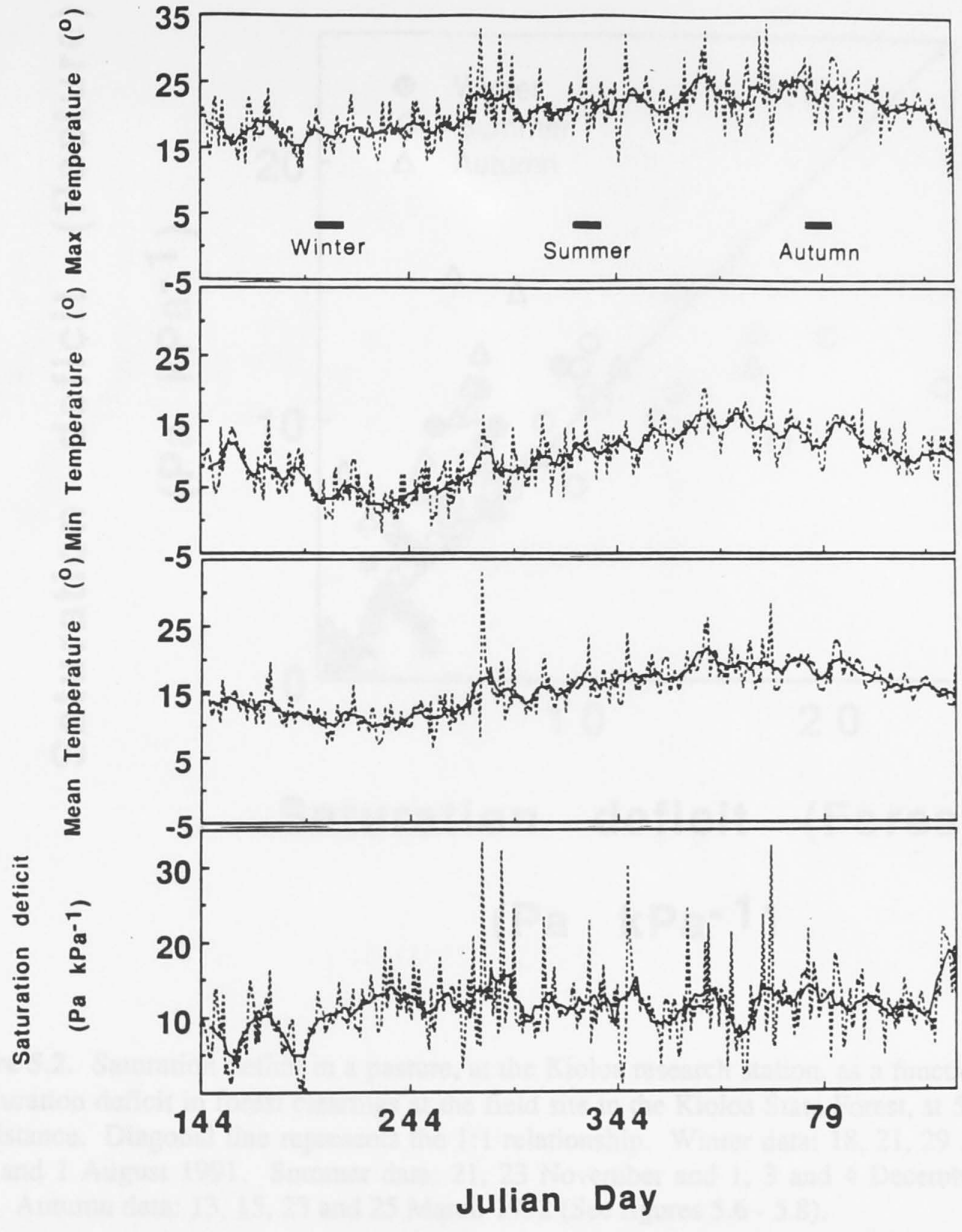


Figure 5.1. Measured maximum, minimum and mean daily air temperature, and saturation deficit in an open pasture at the Kioloa Research Station (dotted lines) from 24 May 1991 to 22 May 1992. Superimposed is the 10-day running mean to show trends in measured parameters (solid line). Winter, summer and autumn seasons refer to measurement periods of whole tree water use at the field plot 5.2 km distance.

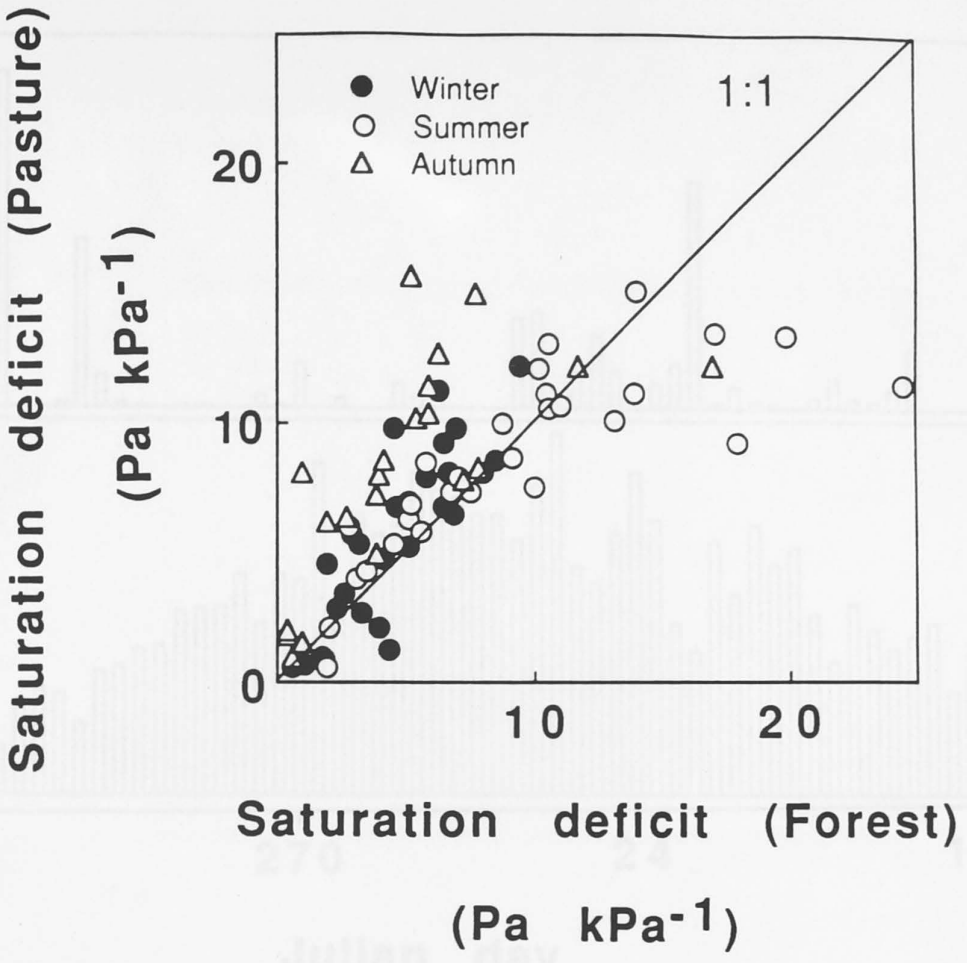


Figure 5.2. Saturation deficit in a pasture, at the Kioloa research station, as a function of saturation deficit in forest clearings at the field site in the Kioloa State Forest, at 5.2 km distance. Diagonal line represents the 1:1 relationship. Winter data: 18, 21, 29 31 July, and 1 August 1991. Summer data: 21, 23 November and 1, 3 and 4 December 1991. Autumn data: 13, 15, 23 and 25 March 1992 (See figures 5.6 - 5.8).

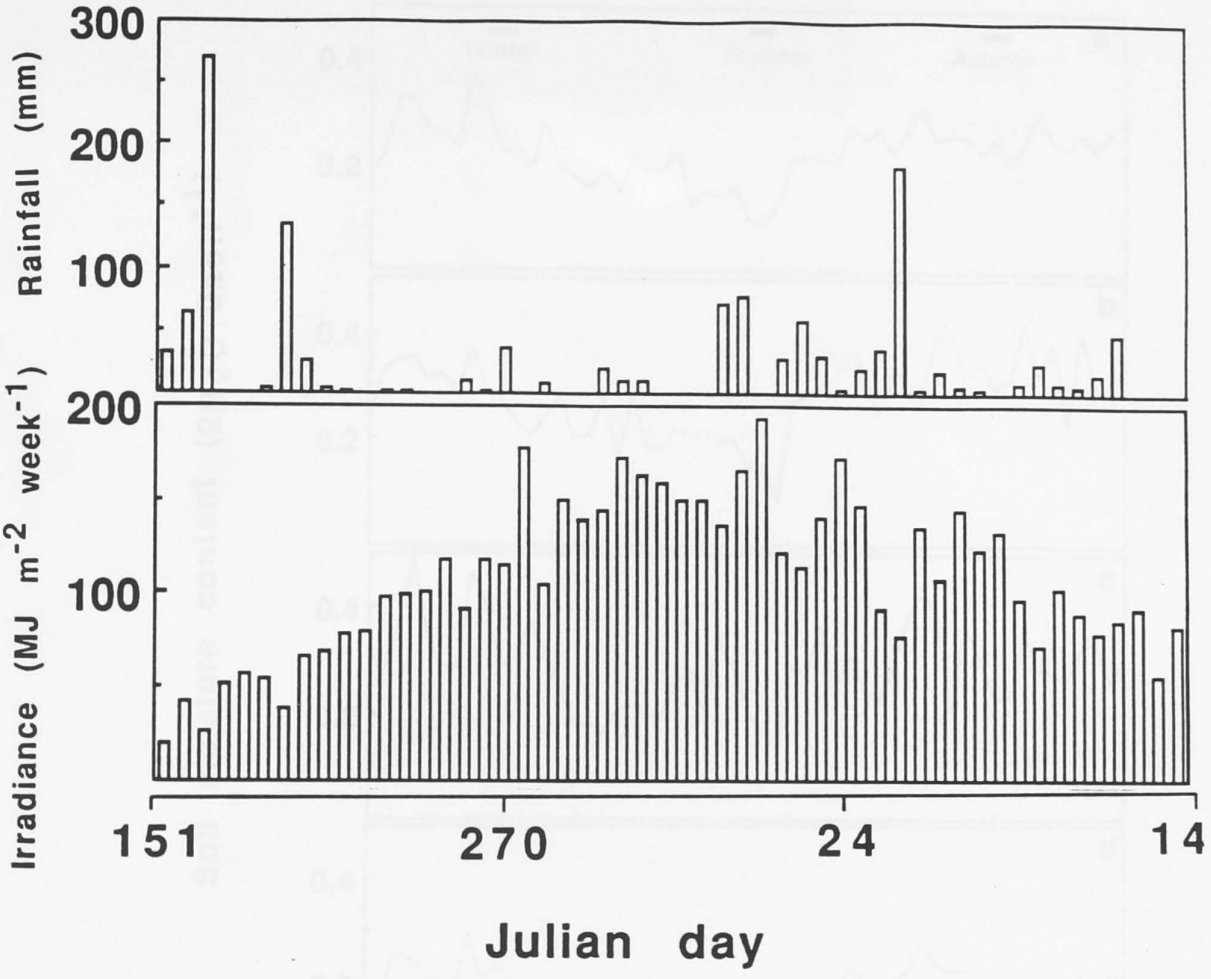


Figure 5.3. Measured weekly total precipitation and total global irradiance incident on a horizontal surface in an open pasture at the Kioloa research station between 24 May 1991 and 22 May 1992.

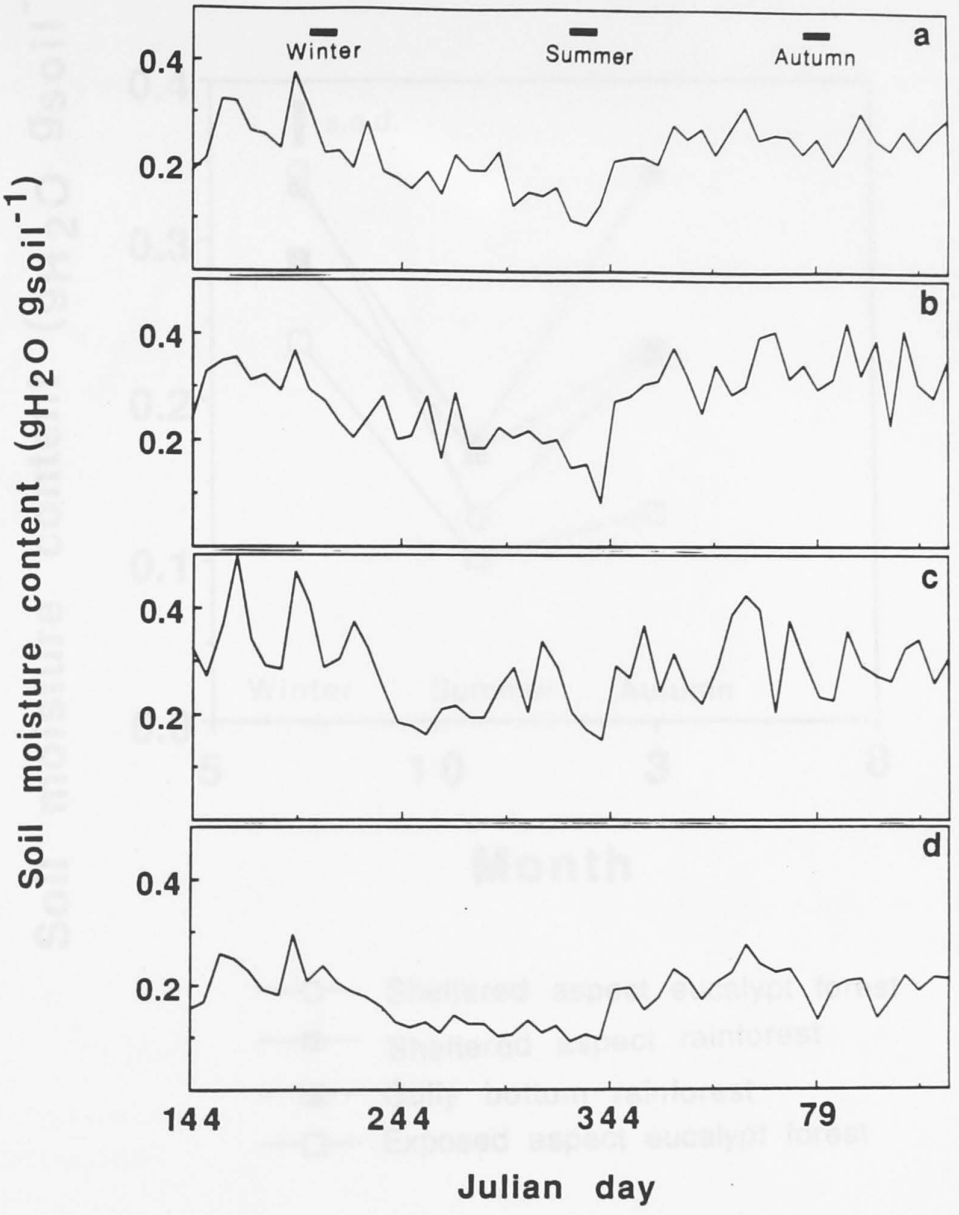


Figure 5.4. Mean weekly soil moisture content (dry weight basis) on four plots at the field site for the period 24 May 1991 to 22 May 1992. (a) sheltered aspect eucalypt forest, (b) sheltered aspect rainforest, (c) gully bottom rainforest, and (d) exposed aspect eucalypt forest. Winter, summer and autumn seasons refer to measurement periods of whole tree water use.

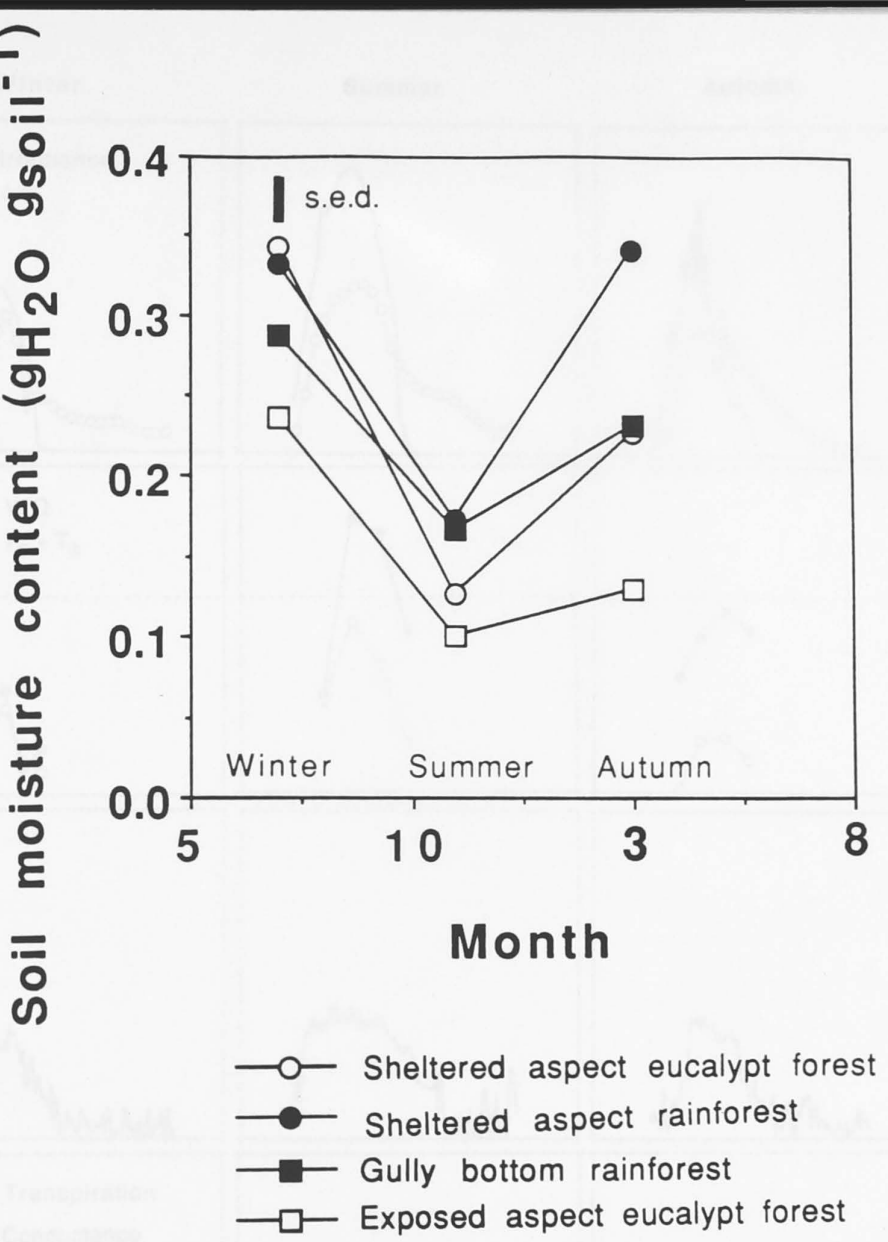


Figure 5.5. Mean soil moisture content on a dry weight basis on four plots at the field site. Means derived from an analysis of variance of data from figure 5.4 for winter, summer and autumn periods corresponding to sap flux measurements. Vertical bar represents standard error of the difference of means.

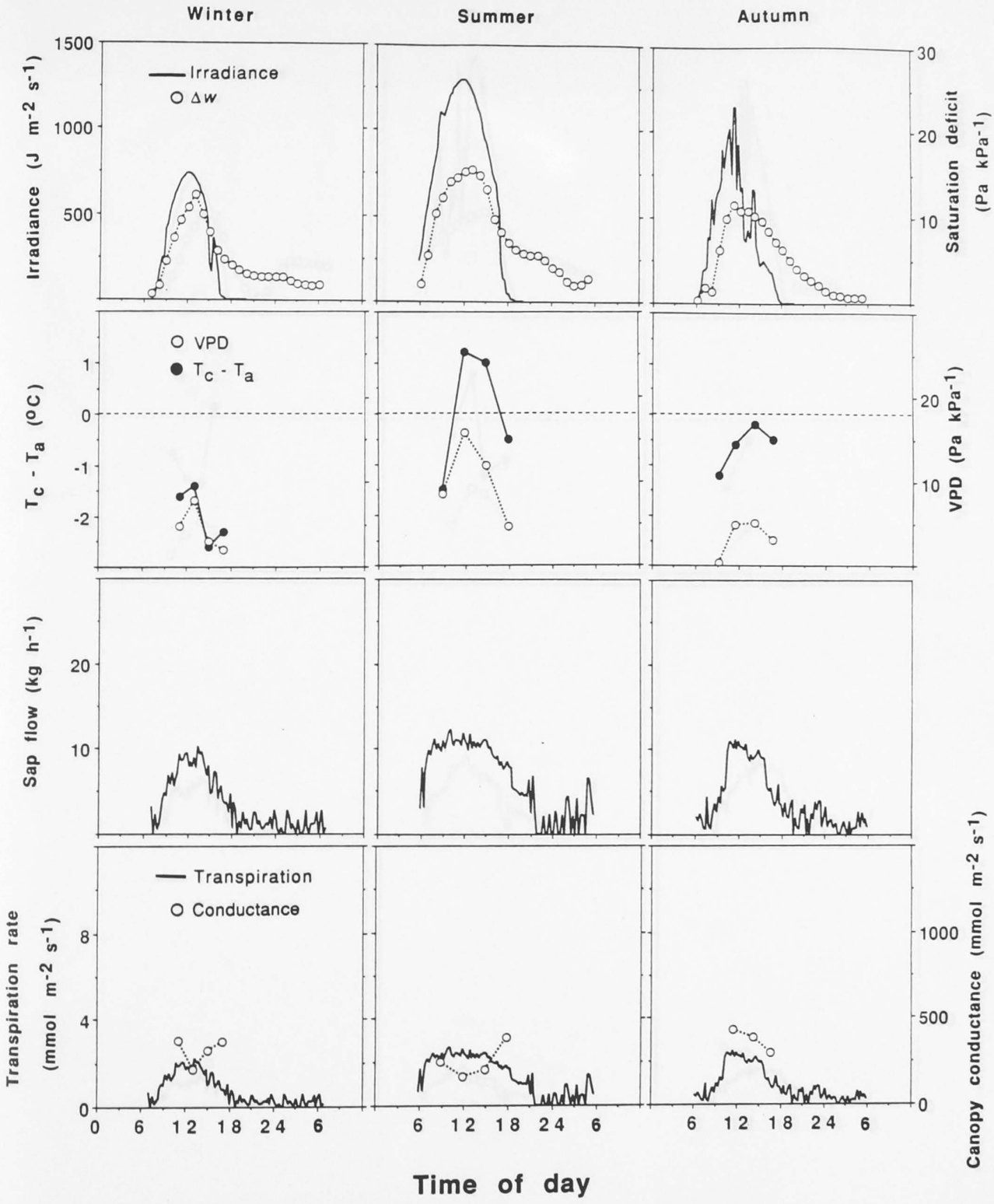


Figure 5.6a. Diurnal variation in global irradiance and saturation deficit (top row), canopy to air temperature (T_C - T_a) and vapour pressure difference (VPD; second row), sap flow (third row), and canopy transpiration rate and canopy conductance to water vapour (fourth row) in a single tree of *Ceratopetalum apetalum*, situated on the gully bottom rainforest plot. Left hand column corresponds to winter measurements (29 July 1991), centre column to summer measurements (1 December 1991) and right hand column to autumn measurements (23 March 1992).

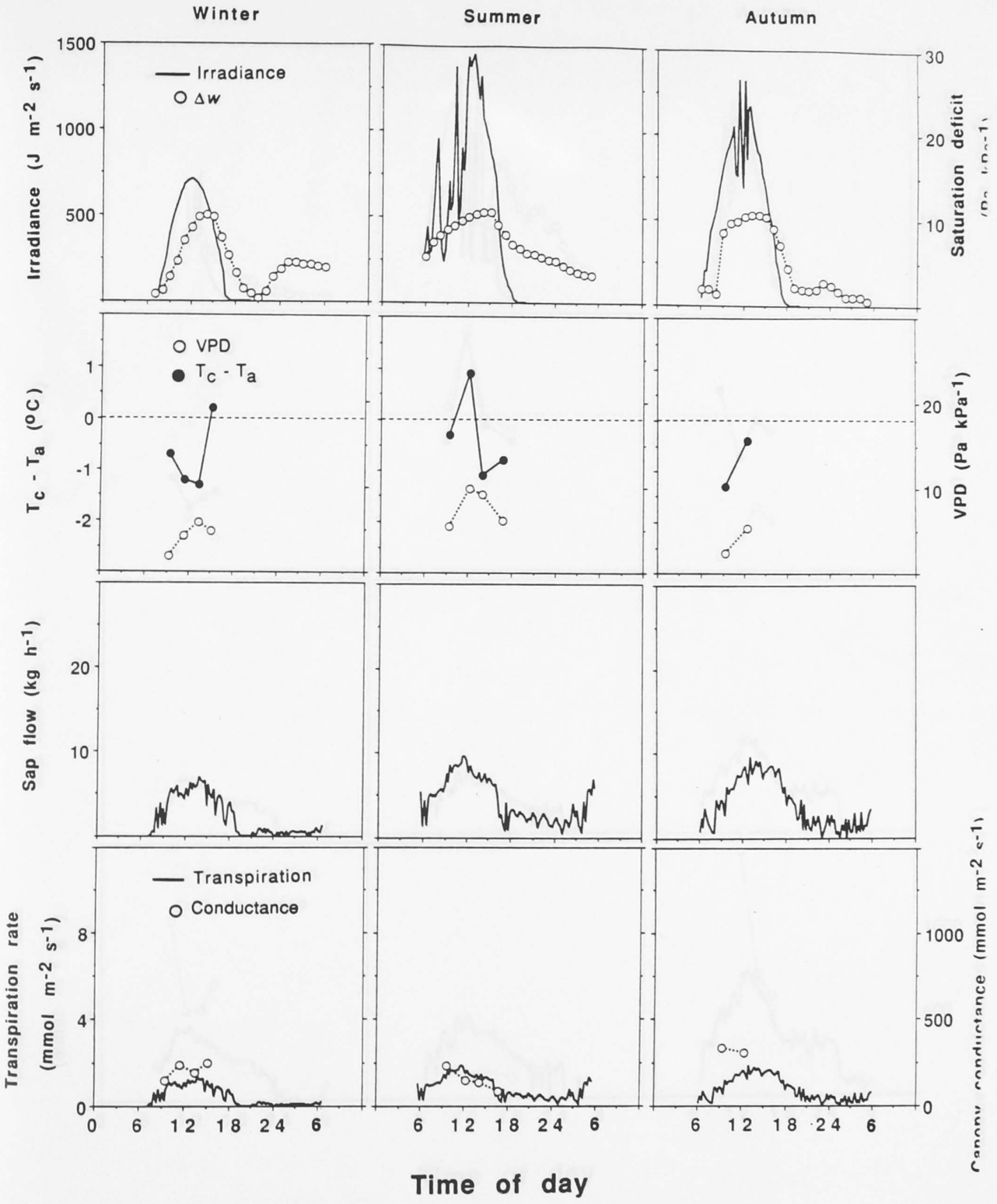


Figure 5.6b. As in Fig. 5.6a, but for *C. apetalum* on the sheltered aspect rainforest plot. The left, centre and right hand columns correspond to winter (18 July 1991), summer (21 November 1991) and autumn (13 March 1992) measurements, respectively.

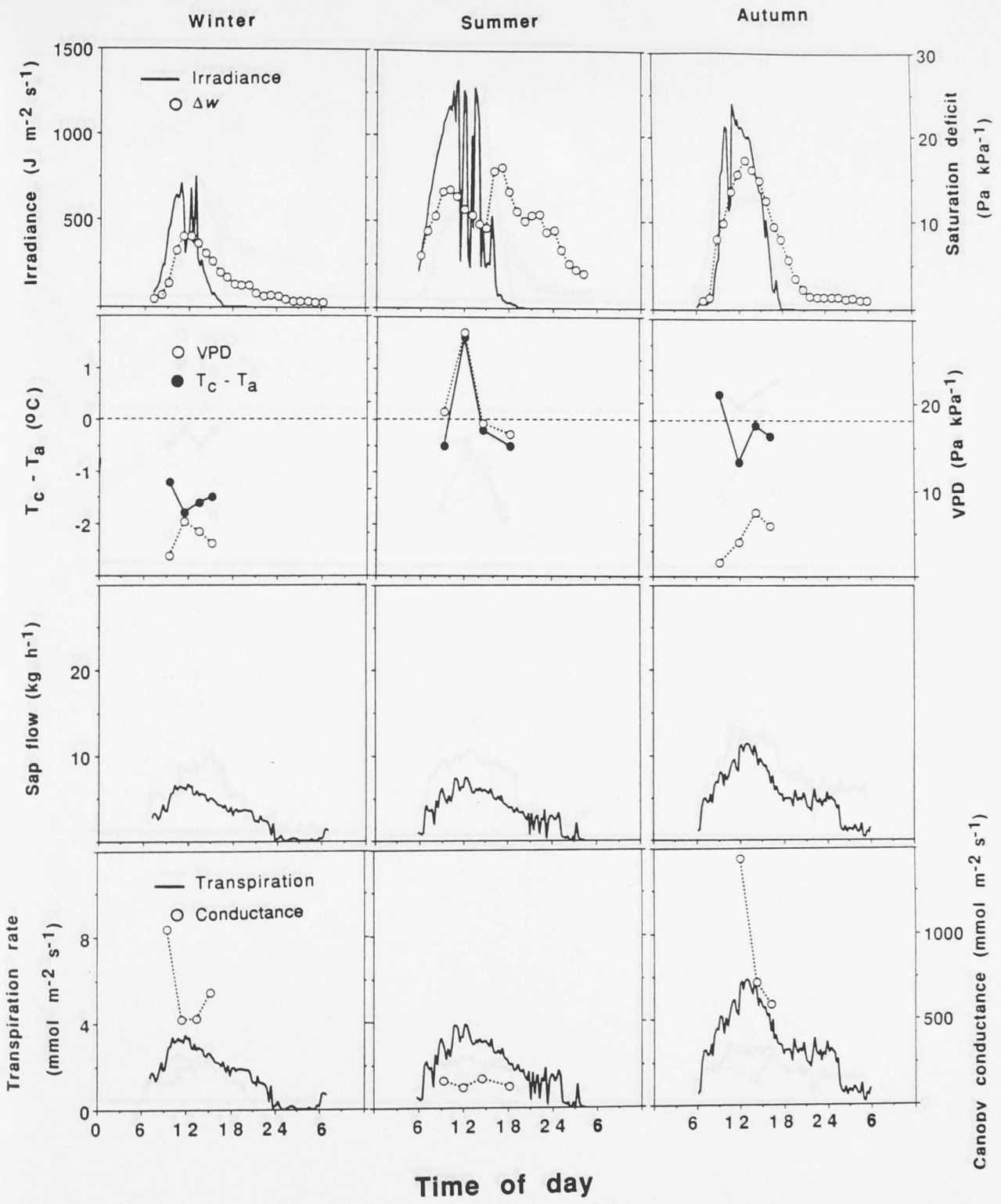


Figure 5.7a. As in Fig. 5.6a, but for *Doryphora sassafras* on the gully bottom rainforest plot. The left, centre and right hand columns correspond to winter (31 July 1991), summer (3 December 1991) and autumn (25 March 1992) measurements, respectively.

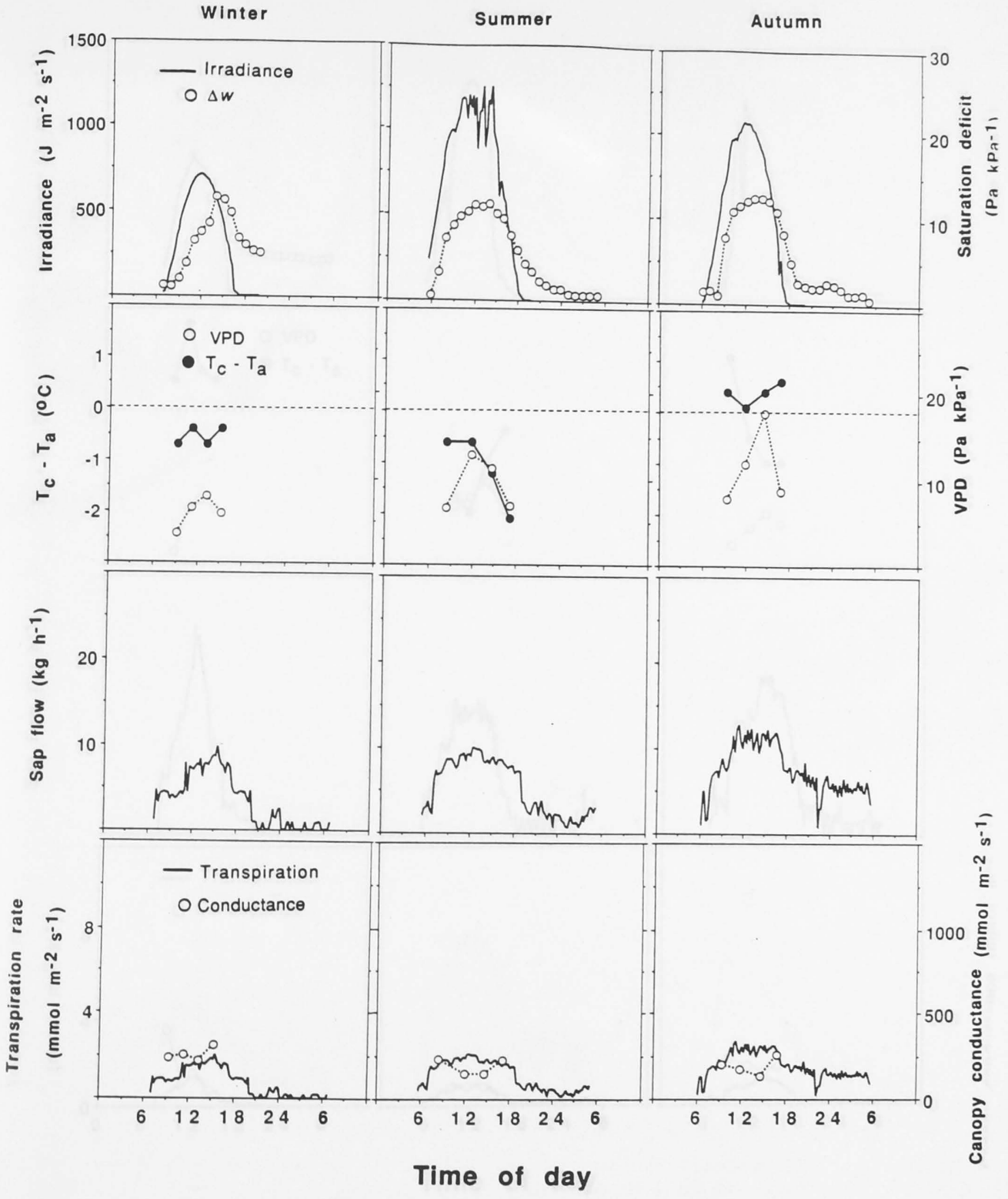


Figure 5.7b. As in Fig. 5.6a, but for *Doryphora sassafras* on the sheltered aspect rainforest plot. The left, centre and right hand columns correspond to winter (21 July 1991), summer (23 November 1991) and autumn (15 March 1992) measurements, respectively.

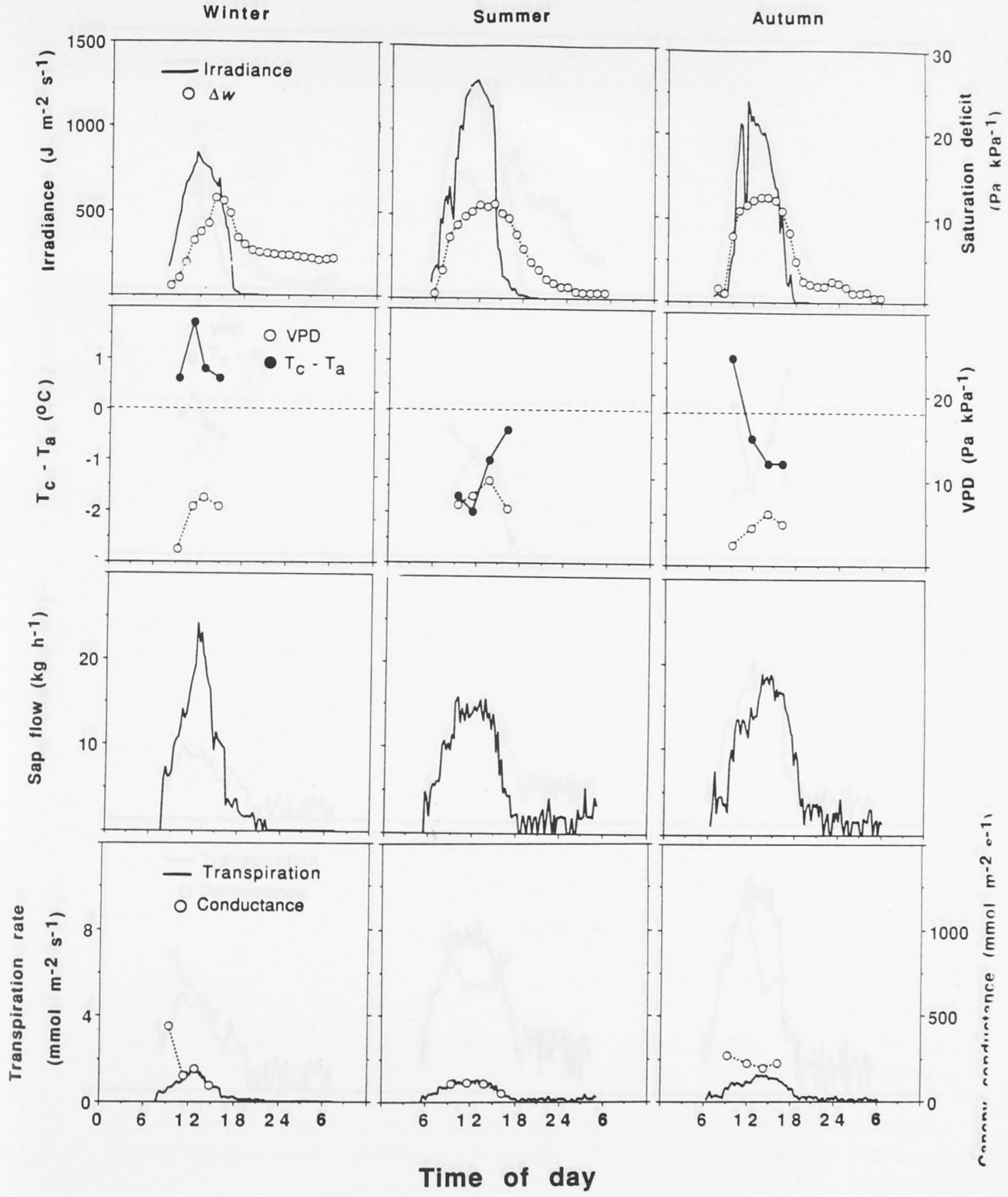


Figure 5.8a As in Fig. 5.6a, but for *Eucalyptus maculata* on the exposed aspect eucalypt plot. The left, centre and right hand columns correspond to winter (1 August 1991), summer (4 December 1991) and autumn (25 March 1992) measurements, respectively.

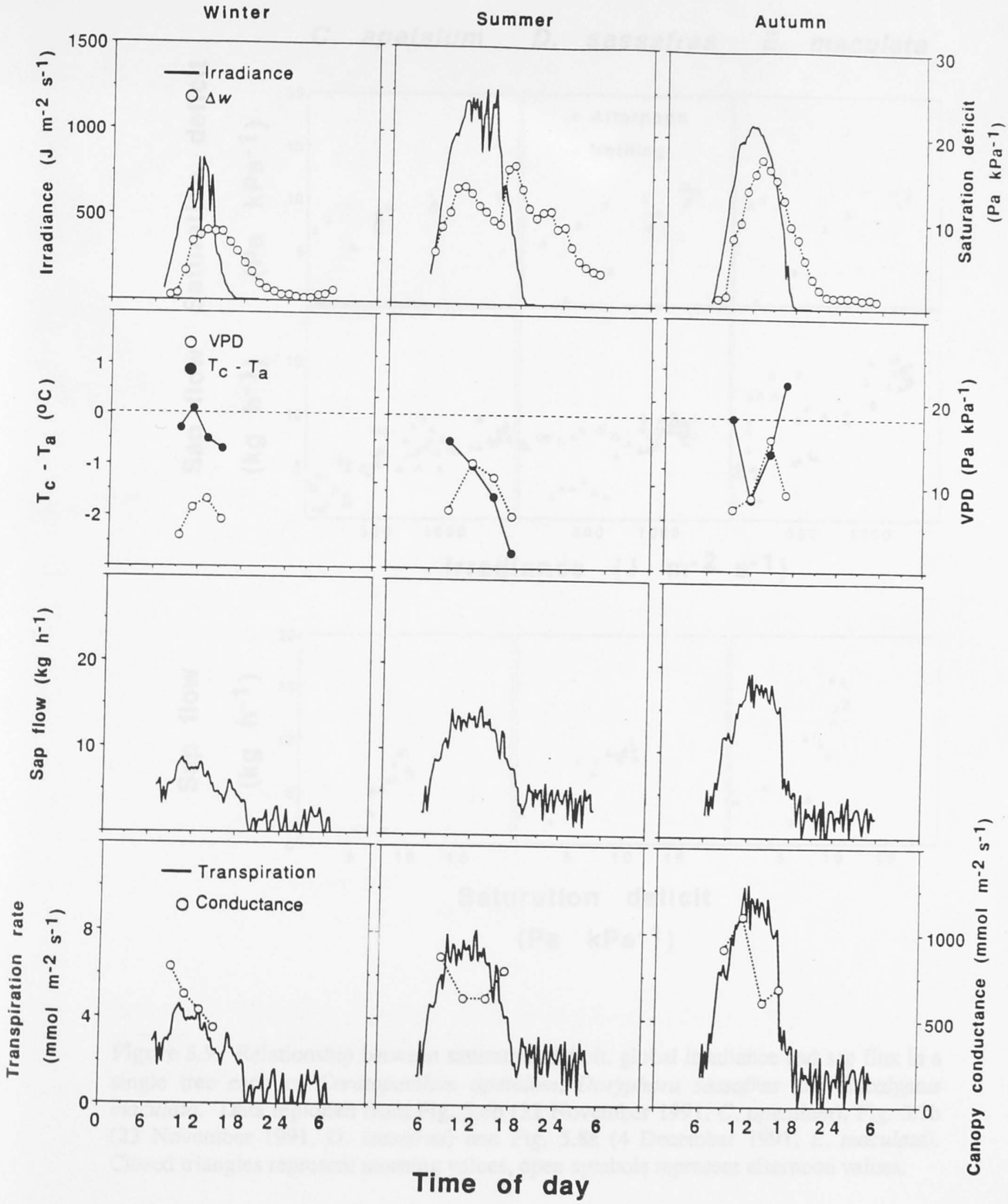


Figure 5.8b. As in Fig. 5.6a, but for *Eucalyptus maculata* on the sheltered aspect eucalypt plot. The left, centre and right hand columns correspond to winter (21 July 1991), summer (23 November 1991) and autumn (15 March 1992) measurements, respectively.

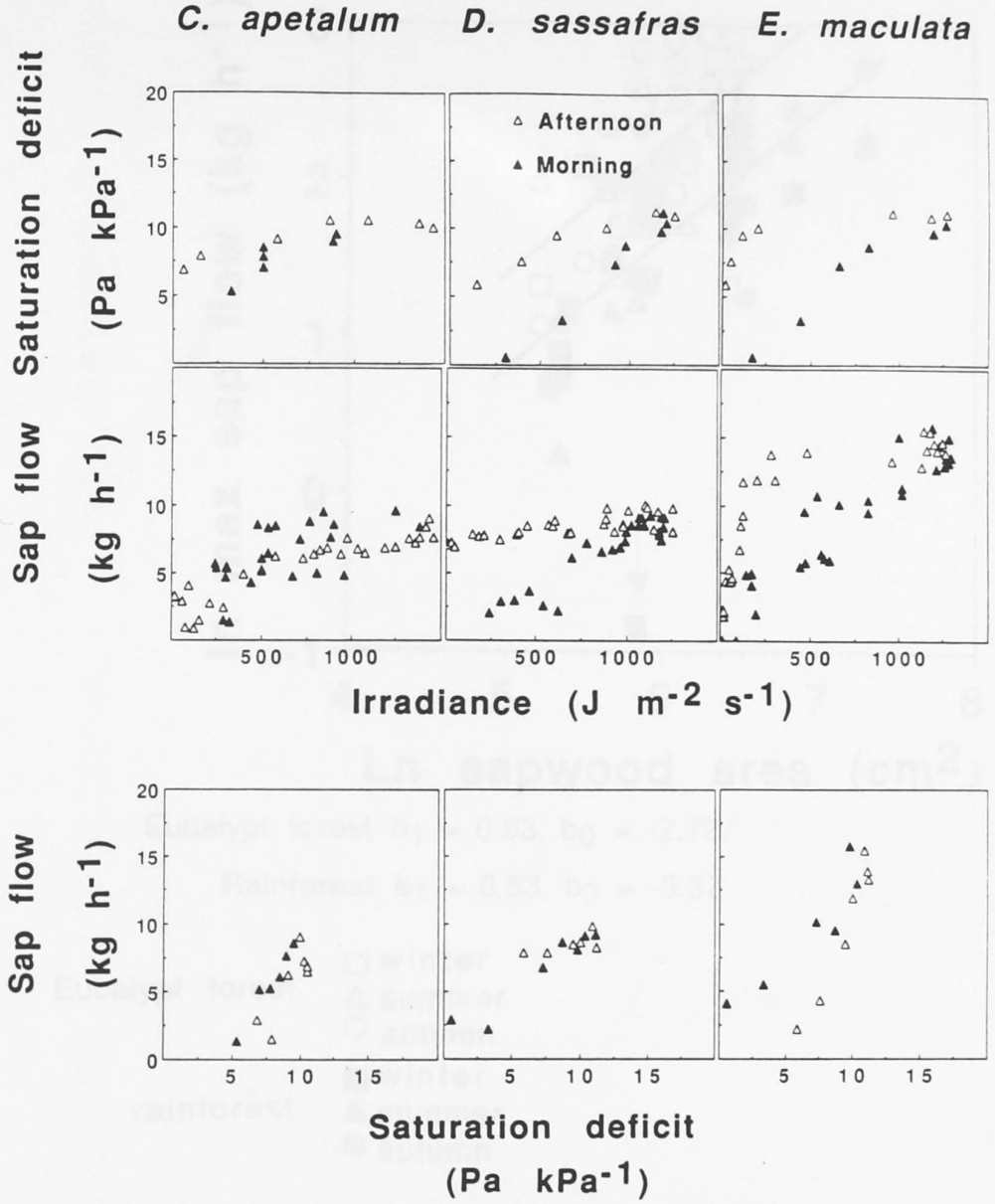


Figure 5.9. Relationship between saturation deficit, global irradiance and sap flux in a single tree each of *Ceratopetalum apetalum, Doryphora sassafras* and *Eucalyptus maculata*. Data replotted from Fig. 5.6b (21 November 1991, *C. apetalum*), Fig. 5.7b (23 November 1991, *D. sassafras*) and Fig. 5.8a (4 December 1991, *E. maculata*). Closed triangles represent morning values, open symbols represent afternoon values.

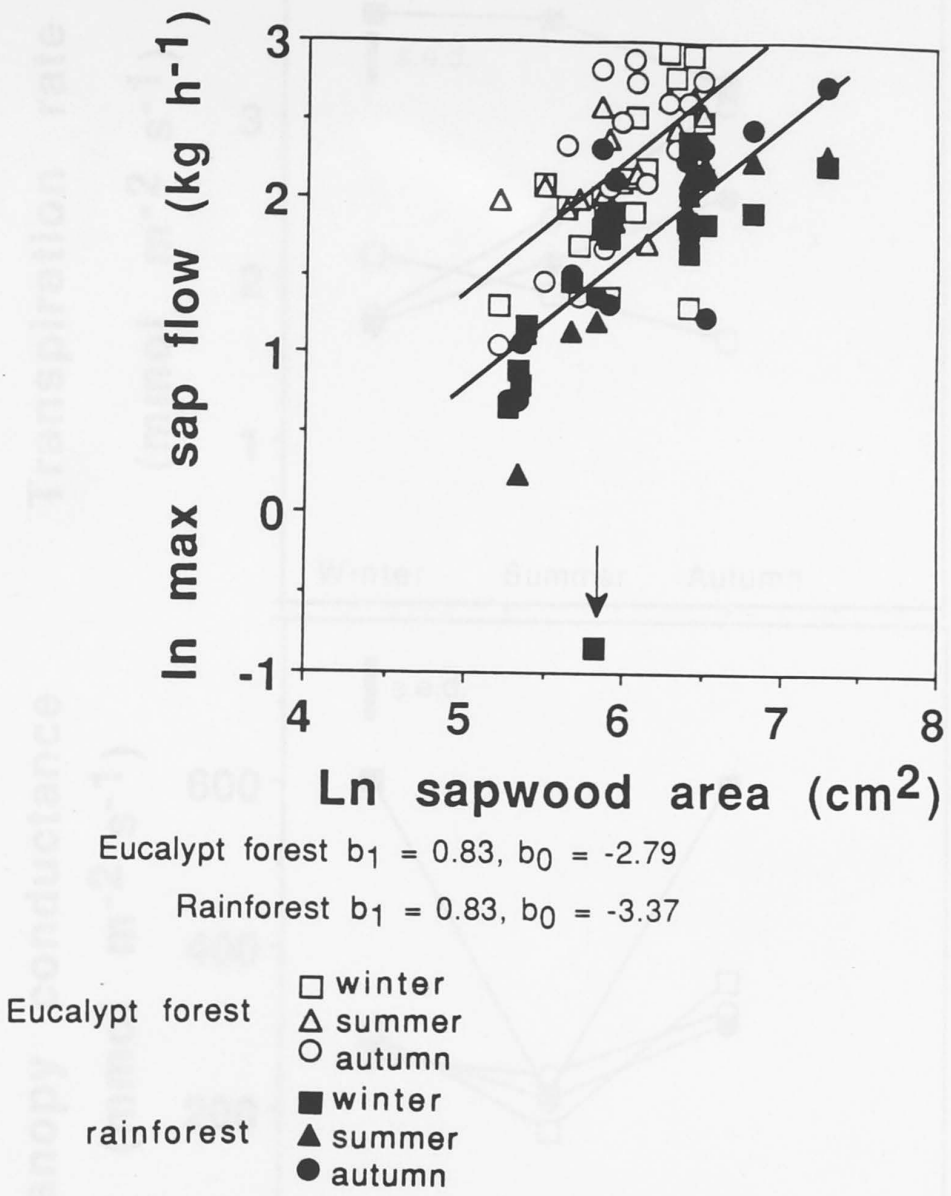


Figure 5.10. Relationship between mean sap flux between 11:00 and 13:00 hours, and sapwood area for rainforest and eucalypt forest trees at the field site. The slope (b_1) and y-intercept (b_0) of each parallel regression line are indicated. The arrow indicates a point removed from regression analysis, corresponding to *Ceratopetalum apetalum* on the sheltered aspect during winter (Tree 1, Table 3.2).

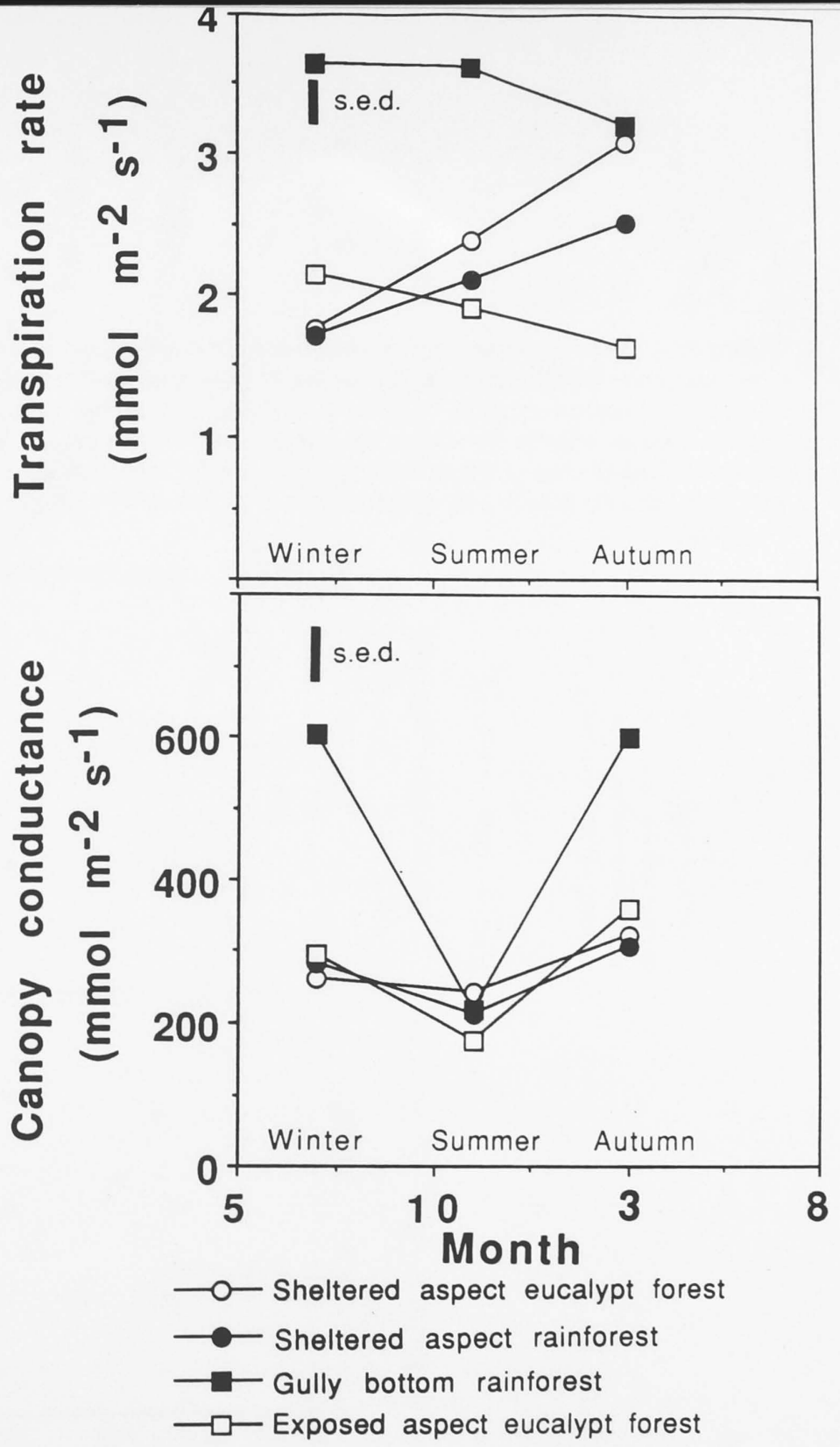
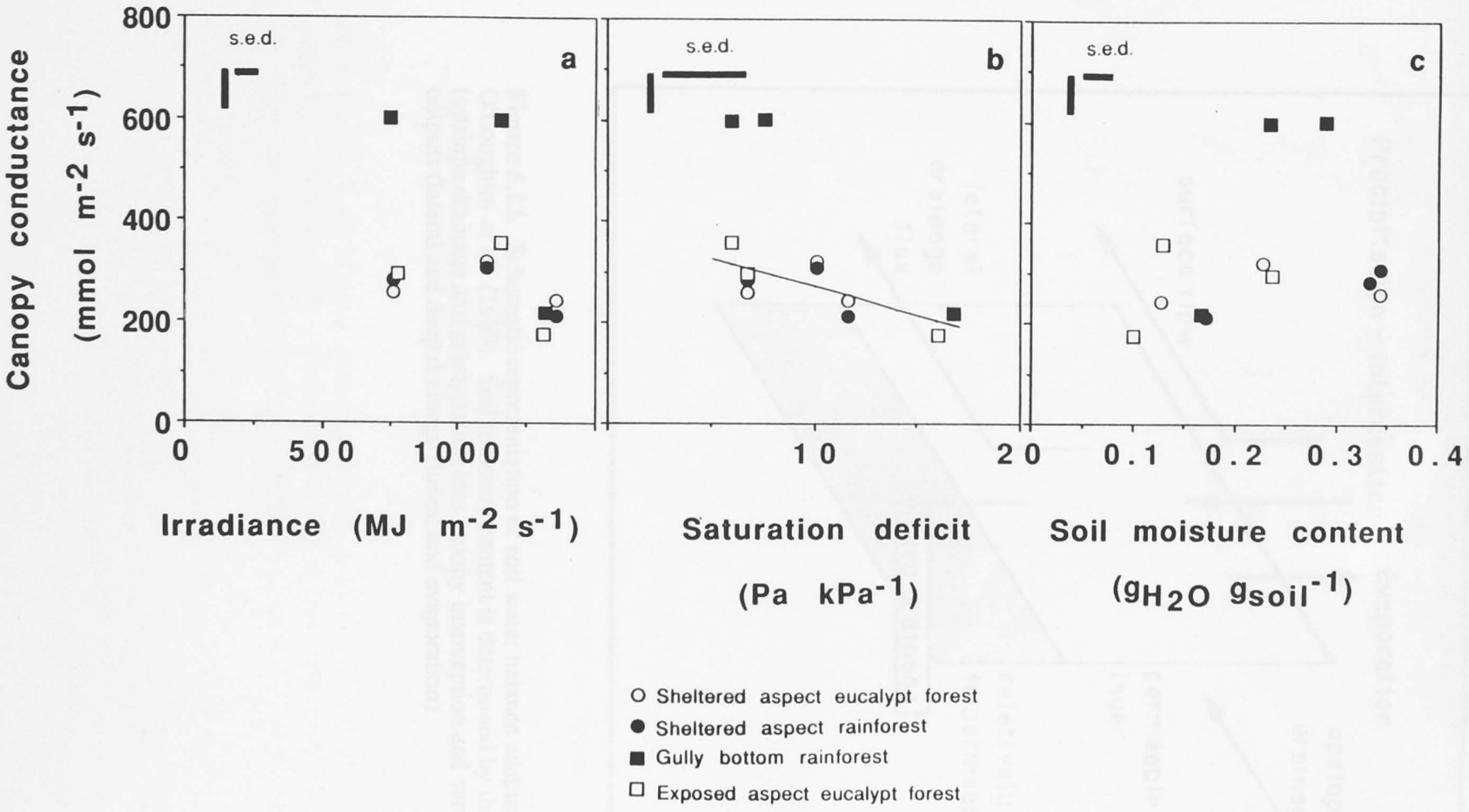


Figure 5.11. Seasonal variation in mean maximum values for (a) canopy transpiration rate, and (b) canopy conductance (on a crown area basis) for the plot x season interaction term in the analysis of variance (Table 5.2). The vertical bar represents the standard error of the difference of means.

Figure 5.12. Mean maximum canopy conductance to water vapour as a function of (a) mean maximum global irradiance, (b) mean maximum saturation deficit, and (c) mean soil moisture content above 0.35 m depth. Averages based on eight trees per plot, derived from an analysis of variance for each parameter. Vertical and horizontal bars represent standard error of the difference of means. The regression line in (b) excludes data from the gully bottom plot in winter and autumn (slope = -11.1; y-intercept = 382; $r^2 = 0.58$).


Canopy conductance
(mmol m-2 s-1)
800
600
400
200
0
s.e.d.
a
0
500
1000
Irradiance (MJ m-2 s-1)
s.e.d.
b
10
20
Saturation deficit
(Pa kPa-1)
s.e.d.
c
0.1
0.2
0.3
0.4
Soil moisture content
(gH2O gsoil-1)
Sheltered aspect eucalypt forest
Sheltered aspect rainforest
Gully bottom rainforest
Exposed aspect eucalypt forest

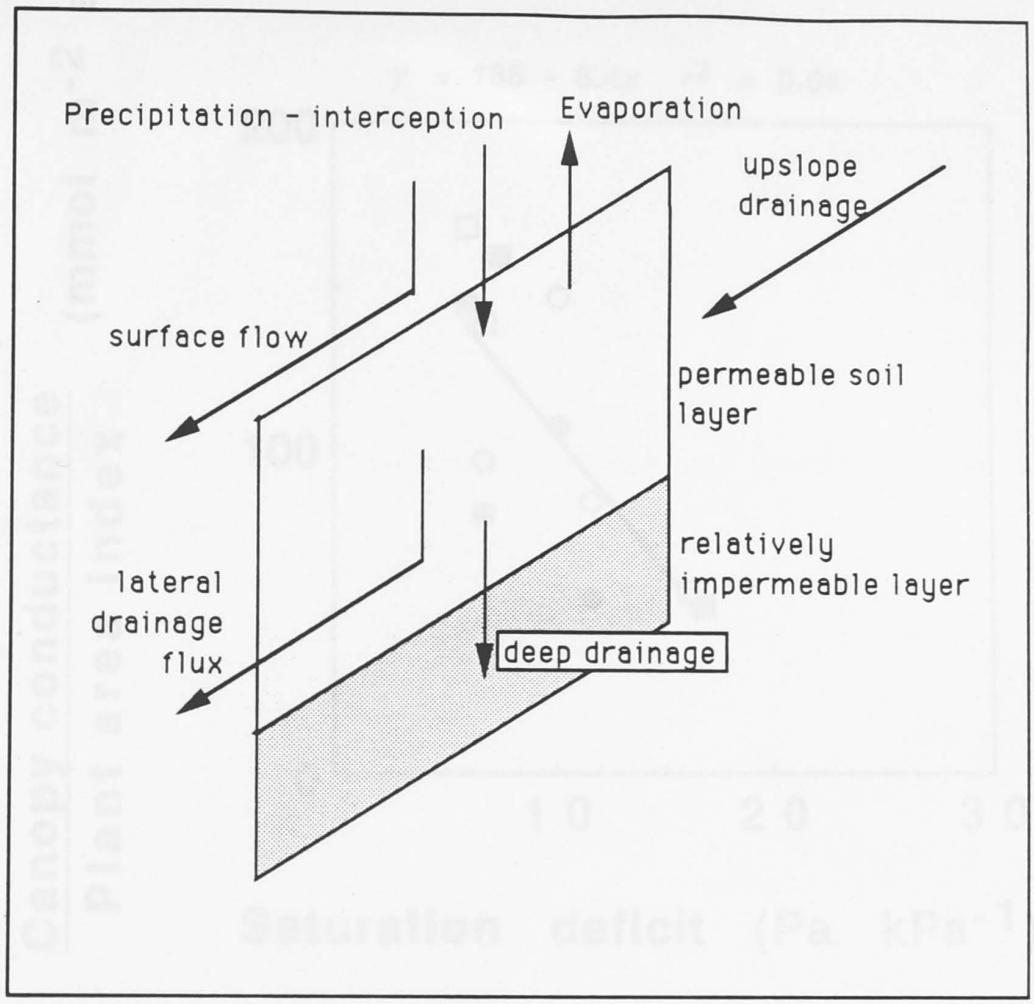


Figure 5.13. Schematic representation of soil water balance adapted from O'Loughlin *et al.* (1989). Soil moisture content is determined by the sum of inputs (upslope drainage and precipitation less canopy interception and surface flow) and outputs (lateral and deep drainage fluxes, and evaporation).

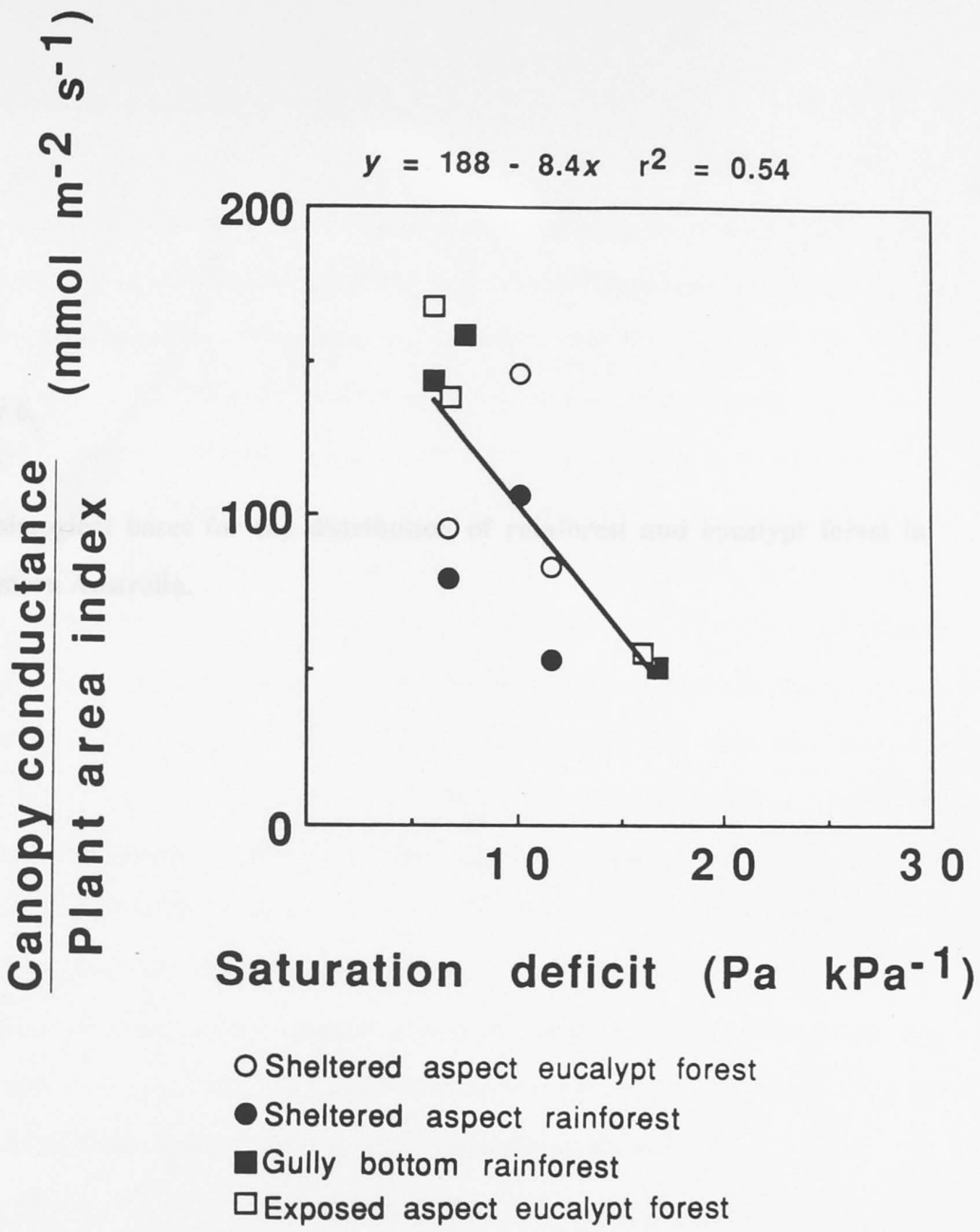


Figure 5.14. Ratio of mean maximum canopy conductance to mean plant area index (from Fig. 3.9) as a function of saturation deficit, in four experimental plots at the field site. The line represents the linear regression with slope = -8.4, y-intercept = 188 (r^2 = 0.54).

Chapter 6.

Ecophysiological bases for the distribution of rainforest and eucalypt forest in southeastern Australia.

Introduction.

The aim of this thesis has been to understand how responses by rainforest and eucalypt forest species to variation in irradiance and water availability were related to the differential distribution of vegetation types with aspect in southeastern New South Wales. Figure 6.1 illustrates the range of spatial and temporal scales over which biological processes operate. Processes at spatial scales less than centimeters and temporal scales less than minutes, such as leaf-level photosynthesis, carbon metabolism, and organelle and biochemical processes, have not been considered in the present study. Rather, in this thesis plant growth, biomass partitioning and water use characteristics at the spatial scale of seedlings and adult trees and at the temporal scale of hours, days and months were investigated. Whitmore (1982) suggested that processes governing establishment, growth and succession in temperate and tropical forests are fundamentally similar world-wide. Consequently, processes controlling vegetation distribution patterns in the present study, may be applicable to other plant communities also distributed differentially along environmental gradients in other locations throughout the world. In this chapter, results from the whole study are integrated into a conceptual model outlining the role of environmental factors in controlling rainforest and eucalypt forest distribution in eastern temperate Australia.

Towards an ecophysiological model of rainforest and eucalypt forest distribution.

A conceptual model, illustrated in Fig. 6.2, outlines the relationships between physical and biological processes operating in mountainous terrain. This section describes the principal features of the model, and later sections expand on processes important at the scale of seedlings and adult trees, incorporating results derived from preceeding chapters.

At the regional scale (10^3 m), precipitation and humidity are important determinants of soil water availability and potential evaporation. Indeed, rainforests in eastern Australia at temperate latitudes are restricted to regions where the mean annual precipitation is in excess of 1000 mm. High precipitation is associated with maritime climates and low saturation deficits. However, variation in regional climate of the order 10^2 to 10^5 years may influence vegetation distribution. Glacial cool-dry periods interspersed with interglacial warm-moist periods, are thought to have influenced the distribution of rainforest and eucalypt forest during the Quaternary Period though such changes are only well documented in northeastern Queensland (Kershaw 1978 and 1985; Hopkins *et al.* 1990 and 1992). Thus, broad scale migration of rainforest vegetation may occur in association with variation in regional climate, although the lag time may be considerable (Hopkins *et al.* 1992). During arid periods rainforest vegetation may persist only in refugia where microenvironments remain suitable for rainforest persistence. Such locations are typically confined gullies and areas supplied by artesian water (Webb and Tracey 1981). By virtue of their microenvironment and vegetation type, refugia are also places of low fire frequency and intensity.

The effect of regional climate on vegetation distribution is mediated by the influence of aspect on ground surface irradiance and associated energy dependent processes, such as soil water evaporation and plant growth. Thus, for a given regional precipitation, soil moisture content will vary throughout a catchment. Exposed aspects tend to have lower soil moisture contents in the surface layers than sheltered aspects (Figures 5.4 and 5.5). Additionally, lateral sub-surface drainage may increase soil moisture contents at the gully bottom. However, water tables and deep soil drainage may increase water availability at depths to which tree roots penetrate, mitigating aspect related differences in water availability to adult trees. Soil nutrient content, largely determined by substrate, may also be influenced by topography (eg. McColl 1969). Thus, positive interactions between nutrient and water availability on plant biomass, such as occurred

in the glasshouse experiments (Table 2.3), may partly explain greater biomass on sheltered aspects reported in some studies (Table 1.1).

At the seedling scale, irradiance, soil moisture content and nutrient availability are strongly influenced by factors controlling the local microenvironment. As size increases, from seedling to sapling and eventually to adult tree, the effect of microenvironment near the soil surface on growth and water use diminishes, whereas the influence of regional climate increases. Eventually, in a canopy strongly coupled to the atmosphere, growth and water use are primarily dependent on regional precipitation and humidity (McNaughton and Jarvis 1983 and 1991; Jarvis 1986) and less dependent on aspect mediated microclimate. Canopy closure has a significant effect on microenvironment near the soil surface. Light interception by the canopy reduces total irradiance but also increases the variability in irradiance at the ground surface (eg. Pearcy 1988). Modification of the light environment by the canopy may then influence soil and air temperature near the ground, thereby influencing soil evaporation and soil moisture content (Chapter 5). Additionally, transpiration from the canopy may alter the humidity of the air within and beneath the canopy (McNaughton and Jarvis 1991). Variation in microenvironment, in particular irradiance, has a profound influence on seedling growth (Chapter 2). Seedlings of rainforest species are adapted to growth under variable and low light environments such as the rainforest understorey. Alternatively, eucalypt species achieve fast growth rates in relatively high light environments such as in open sites or beneath the eucalypt canopy on exposed aspects.

In forests, the strength of the feedback loops between the atmosphere and forest growth and water use are dependent on the degree of coupling between plants and climate, and on the scale and structure of the stand (Jarvis 1986; Whitehead 1988; Whitehead and Hinckley 1991; McNaughton and Jarvis 1991). Jarvis (1986) summarised feedback processes controlling carbon and water fluxes in forest canopies, thus:

> "(1) The properties of the stand are not just the simple sum of the properties of the individuals;
>
> (2) The environment is perceived at the scale of the organ, but what is perceived depends on the structure of the stand;
>
> (3) The individual responds at the scale of the organ, but the consequences [for the individual] depend on the responses of all other individuals."

These feedback processess may also be applicable to plant growth and water use in rainforest and eucalypt forest seedlings and adult trees in southeastern New South Wales. Thus, at the scale of the canopy, plant responses at the tree and leaf level are strongly influenced by regional climate because of strong coupling between the canopy and the atmosphere. However, at the scale of the seedling, plant responses are strongly influenced by microclimate because of poor coupling between the seedling and the atmosphere.

Fire is included in the conceptual model (Fig. 6.2), and influences the probability of plant mortality. However, the influence of fire on vegetation distribution is mediated by forest type and microenvironment. Evidence of past fires may be found in both rainforests and eucalypt forests on both exposed and sheltered aspects throughout southeastern New South Wales. However, fire frequency and intensity, as indicated by flame scorch and fire scar heights on tree trunks, are higher in eucalypt forest than in rainforest. Fuel quantity and flammability are influenced by vegetation type, whereas fuel moisture content may be influenced by ground surface irradiance and soil moisture. Because of the positive feedback of forest type on fire frequency and intensity (Mutch 1970), fires will be more frequent and more intense in eucalypt forest than rainforest and more intense on exposed than sheltered aspects. Therefore, the influence of fire on rainforest vegetation will be greatest at the boundary between forest types. In locations of high fire frequency and intensity, such as exposed aspects, the ecotone between vegetation types is well defined, whereas on sheltered aspects, more diffuse vegetation

boundaries are oberved (eg. Ash 1988; Unwin 1989a). Thus, on exposed aspects the microenvironment may be unfavourable for establishment of rainforest species into burned areas contributing to the abrupt nature of the rainforest boundary, whereas on sheltered aspects a more favourable microenvironment may increase rainforest seedling establishment thereby creating a more diffuse boundary.

The time scale of forest growth and forest dynamics is of the order of 10^1 - 10^3 years. Therefore simulation modelling techniques will be necessary to investigate the validity of the conceptual model illustrated in Figure 6.2. Such an investigation is beyond the scope of this thesis. However, future work may be directed towards parameterisationof the conceptualmodel using (a) forest growth and productivity sub-models to incorporate plant growth and forest production (eg. McMurtrie *et al.* 1990), (b) hydrological modelling concepts to determine site water balance (eg. Moore *et al.* 1991), (c) ecological sub-models incorporating statistical probabilities of mortality and fire (eg. Noble and Slatyer 1980), and (d) fire behaviour sub-models (eg. Luke and McArthur 1978) to determine the role of fire on vegetation distribution. Such a modelling procedure may provide the only reasonable means of integrating mechanistic processes governing rainforest and eucalypt forest vegetation dynamics throughout eastern Australia.

Processes at the seedling scale.

(a) Seedling growth and biomass partitioning.

Plant biomass production is determined by the amount of carbohydrate supplied from photosynthesis less that lost by respiration, and the amount of water and nutrients available to the plant. A plant may increase the supply of carbohydrate, water or nutrients by either allocating biomass to different resource acquisition structures

(morphological plasticity) or by variation in the rates of carbon gain and loss (physiological plasticity). The relationship between carbon, water and nutrient fluxes, and biomass allocation are summarised in Figure 6.3. Assimilation of carbon dioxide by photosynthesis supplies carbohydrate which is used in growth and maintenance respiration. Control over biomass allocation to root and shoot structures may be dependent on the rates of water and nutrient uptake from the soil, on carbohydrate supply from the leaves, and on the demand for resources within the plant (Thornley 1972; Bastow-Wilson 1988; Farrar 1989). When resources are limiting, plants may allocate biomass to organs which increase supply of that limiting resource (Grime *et al.* 1986; Bastow-Wilson 1988). Thus, biomass allocation to roots may occur when water and nutrient availability are low. Alternatively, biomass allocation to leaves in response to low irradiance may increase light interception contributing to greater carbon gain. Increased height growth by allocation to stems may also increase net radiation interception if the plant is able to grow above others or into adjacent gaps. Future plant survival may be dependent on partitioning strategies which are influenced in the short term by genetic control and the environment. However, biomass partitioning may occur at a cost. Allocation to leaves may increase the potential evaporative surface area, thereby increasing the demand for water by the plant (Schulze *et al.* 1983), and partitioning to non-photosynthetic structures may increase maintenance respiration, thereby reducing carbohydrate available for plant growth (Givnish 1988).

Plant biomass and biomass allocation differed between pot grown rainforest and eucalypt forest species under different light, water and nutrient treatments (Chapter 2). These results concur with the first hypothesis in Chapter 1, which proposed that plant growth and biomass partitioning would vary between rainforest and eucalypt species in such a way as to enhance growth in eucalypts at high light and low soil moisture, but favour growth in rainforest species under low light and high soil moisture. In general, greater biomass was observed in eucalypt species, which occur naturally in high light environments, when resources were abundant (Figs. 2.1 and 2.4). However, plants

responded primarily to irradiance rather than to water or nutrient treatments. Additionally, eucalypts displayed greater morphological plasticity in terms of leaf area ratio and specific leaf weight in response to different treatments levels (Figs. 2.2 and 2.5) than did rainforest species. Greater biomass was observed in eucalypt species under conditions similar to those found on exposed aspects, whereas greater biomass in rainforest species was observed under conditions similar to those on sheltered aspects.

At the seedling and sapling scale, availabilty of resources to a plant may be a function of plant size (Goldberg and Werner 1983; Gaudet and Keddy 1988), the space available and the activities of neighbouring plants (Benjamin and Hardwick 1986). Thus, within a plant community, high growth rates may imply greater resource capture and increased survival (Grime *et al.* 1986). Three factors may influence seedling size. Firstly, differences in seed size may influence post-germination seedling biomass, particularly in low light environments (Foster 1986; Piper 1986; Osunkoya 1992). Secondly, variation in the onset of growth or the period over which growth is maintained may influence final biomass at the end of the growing season. Thirdly, differences in inherent growth rates may influence biomass. Differences in plant biomass between species may influence competitive outcomes by reducing space available to neighbours (Schulze *et al.* 1986) and depleting edaphic resources (Grime *et al.* 1986). Thus, larger plants may command greater soil and aerial volumes which increase resource supply leading to greater competitiveness. Greater acquisition of resources may be acheived by (a) high proportional allocation to roots, (b) extensive root systems exploiting large soil volumes, and (c) maximisation of light interception by allocation to stem height and leaf area (Grime *et al.* 1986; Aerts *et al.* 1991). Similar features were observed in seedlings of eucalypt species, which may imply greater competitiveness for resources than in seedlings of rainforest species. However, growth rates may vary with variation in resources, thereby changing competitive outcomes under different environmental conditions (Van Andel and Biere 1989). Thus, seedlings of eucalypt species may be more competitive than rainforest species providing that irradiance is high, but the

reverse may occur at irradiances below 20% sunlight (approximately 430 μmol photons m^{-2} s^{-1}).

(b) Seedling water use characterisitcs.

Inherent differences in transpiration rates per unit leaf area were expected between rainforest and eucalypt species because of presumed differences in soil moisture contents between exposed and shaded aspects. However, in pot grown plants, no differences were observed in transpiration rates between rainforest and eucalypt species when water was abundant, despite 17 weeks previous growth under different light and water treatments (Fig. 2.7). Transpiration rates are dependent on stomatal control of water vapour transfer, the evaporative demand and the supply of water to leaves. In the present study, similar transpiration rates per unit leaf area under different light and water treatments were associated with differences in root mass per unit leaf area (Fig. 2.5). Thus, water supply to leaves for transpiration under conditions of high evaporative demand at high irradiance, may have been increased by greater biomass allocation to roots (Passioura 1982). However, there were no differences in root mass per unit leaf area between rainforest and eucalypt species or in rates of water uptake between plants grown under medium and high light treatments (Fig. 2.7). Thus, similar transpiration rates between seedlings of rainforest and eucalypt species in the present work, may be due in part, to similarities in the proportion of water supply tissues (roots) in relation to water loss tissues (leaves).

In the field, seedlings growing on exposed aspects may be subjected to lower soil moisture in the surface layers (Fig. 5.5) than those growing at the gully bottom or on sheltered aspects. However, the temporal variability in soil moisture at any location is greater than the spatial variability between aspects. Therefore, the interaction between

moisture availability and high irradiance on exposed aspects, may be more important in determining seedling growth and survival, than soil moisture content alone.

Under conditions of low soil moisture content, high saturation deficit and high irradiance, seedlings of eucalypt species which possess high rates of growth, may be advantaged over rainforest species. This is because rapid rates of root growth may extend roots deeper into the soil profile, where water supply is less variable (Grime *et al.* 1986). Thus, seedling survival may be increased by decreasing the period in which water supply is derived from near the soil surface. Additionally, root architecture influences plant water uptake (Caldwell and Richards 1986; Fenner 1987). The thinner and more ramified root systems observed in eucalypt seedlings may be more effective in extracting water from the soil profile than the thick, laterally spreading and shallow root systems of rainforest species.

(c) Seedling growth and the influence of fire.

The thermal conductivity of bark is approximately similar between all species (Martin 1963). For a given fire intensity and duration, bark thickness is the principal factor determining cambium temperature (Vines 1968), although fire behaviour may be modified by bark flammibility (Gill and Ashton 1968). Thus, thick barked species are typically less fire sensitive than thin bark species (Gill 1975). Seedlings of both eucalypt forest (eg. Bowman and Kirkpatrick 1986) and rainforest (eg. Stocker and Mott 1981; Unwin 1989b) are sensitive to fire. Thin bark in seedlings and saplings results in higher cambium temperatures and a higher mortality for a given fire intensity, than in larger saplings or adult trees (Vines 1968; Gill and Ashton 1968). Furthermore, fire intensity and duration are a function of fuel quantity, flammability and moisture content (Cheney 1981). Consequently, hotter and more frequent fires occur on exposed aspects (Yates 1989). Thus, for a given bark thickness, higher cambium temperatures

may occur in locations of higher fuel load and lower fuel moisture content. Under these conditions, high rates of seedling and sapling growth, such as in eucalypt species, may be important in rapidly attaining protective bark thereby reducing the period in which seedlings are susceptible to fire. Additionally, adaptive features such as epicormic buds and lignotubers may contribute to fire resistence in eucalypt species (McArthur 1968; Cremer 1972; Gill 1981). Slower rates of seedling growth and generally thinner bark in rainforest species, may result in longer periods of fire susceptability thereby reducing survival on exposed aspects. Thus, interactions between fire behaviour and plant growth on natural light and water gradients may also contribute to the differential distribution of rainforest and eucalypt forest of eastern Australia.

Four generalisations can be drawn from both the experimental studies on growth of rainforest and euclaypt forest species (Chapter 2) and from previous studies which may be important in determining forest distribution patterns:

(1) Eucalypts do not germinate under rainforest canopies (eg. Ashton 1981b; Unwin 1989).

(2) On all aspects in open sites, eucalypts can establish and will maintain high rates of growth eventually forming an overstorey which may persist for the life of these trees (ie. 200 - 350 years; Jackson 1968; Ashton 1981b).

(3) On exposed aspects, seedlings of rainforest species may be disadvantaged under conditions of chronic soil moisture deficit and high potential evaporation rates by restricted root systems and slow growth rates.

(4) On sheltered aspects in open sites, the probability of drought and fire induced mortality in rainforest species may be lower than on exposed aspects, but growth rates

are slower than eucalypt species. Eventually on sheltered aspects, canopy closure by rainforest species occurs which then excludes eucalypt germination.

(5) Most rainforest species are adapted to germination and growth in low light environments beneath rainforest canopies, though many require gaps (Bazzaz and Pickett 1980). In contrast, eucalypt forest species are adapted to germination and growth under higher irradiance, such as occur on open sites or beneath eucalypt canopies on exposed aspects.

The feedback between forest type on both fire behaviour and seedling growth, may reinforce and stabilise vegetation distribution patterns and determine the abruptness of vegetation boundaries. Disturbance may contribute to the maintenance of a mixed forest or promote progression towards eucalypt forest, depending on the interaction between aspect microenvironment and vegetation type. Outside the shaded microenvironment of the rainforest understorey, ecotonal species utilise the high light conditions for establishment and growth (Turton and Duff 1992), however these species may be excluded from eucalypt forest by their intolerance to fires and drought.

Processes at the forest scale.

At the forest scale, partitioning of resources into canopy leaf area may be partly controlled by site water availability and atmospheric humidity. The linear relationships between sapwood area and leaf area of the canopy observed for many tree species (Waring 1983), may indicate a relationship between water supply to, and water loss from leaves (Whitehead 1985). Maximum leaf area in mature conifer forests of the Pacific Northwest, North America, has been related to evaporative demand and soil water availability, independent of species composition of the forest (Grier and Running 1977). Gholz (1982) concluded that the relationship between leaf area and site moisture

in Pacific Northwest coniferous forests, reflected a response to climate and hydrological conditions over the longer term, rather than annual fluctuations in precipitation and climate. Similar relationships between foliage area and climate have also been reported for Australian plant communites (Specht 1972, 1983; Specht and Morgan 1981). Sites of lower evaporative demand and/or higher soil water availability may support vegetation of higher foliage projective cover, essentially a measure of plant area index. On exposed and sheltered aspects in South Australia, Specht (1972) demonstrated that differences in soil water balance and potential evaporation at the ground surface were related to variation in foliage projective cover of the overstorey irrespective of species composition. Thus, maximum foliage area index on any site may be determined by the relationship between humidity and soil moisture. A functional relationship between site water balance, leaf area and sapwood area seems reasonable considering that leaf area may be an important determinant of plant transpiration (Whitehead 1988).

In the present study, differences in canopy structure between rainforest and eucalypt forest were expected in association with apparent differences in water availability on exposed and sheltered aspects. Additionally, it was expected that differences in canopy structure may be manifest as differences in canopy transpiration rates. Measurement of plant area index using the hemispherical photographic technique (Chapter 3) were ranked: gully bottom rainforest plot > sheltered aspect rainforest plot > both eucalypt forest plots. This ranking was consistent with the presumed water availability on each site. Furthermore, mean plant area index was linearly related to the sapwood area per unit crown area (Fig. 3.12) suggesting a functional relationship between leaf area and sapwood area, independent of species (Jordan and Kline 1977; Whitehead 1988) and consistent with other studies (Grier and Running 1977; Gholz 1982; Waring 1983). However, in the present work, neither the mean maximum canopy transpiration rate per unit crown area (Fig, 5.11a), nor the average soil moisture content in the surface layers on each plot (Fig. 5.5), were related to mean plant area index (Fig. 6.4). This result concurs with Honeysett *et al.* (1992) who found no relationship between transpiration

and leaf area index in *Eucalyptus nitens* and *Eucalyptus delegatensis* despite a two-fold variation in leaf area index between species, but disagrees with results from Dunin and Aston (1984) for regenerating *E. maculata* forest, and from Greenwood *et al.* (1985) for five eucalypt species in a young plantation forest.

The second hypothesis (Chapter 1) proposed that differences in canopy structure between rainforest and eucalypt forest would be related to differences in canopy transpiration. The results from the field studies in Chapters 3 and 5 in part concur with this hypothesis. Canopy conductance and transpiration in rainforest at the gully bottom were dependent on leaf area, stomatal response to humidity and plant water availability. On slopes above the gully bottom, maximum canopy transpiration rates in both rainforest and eucalypt forest were less dependent on the canopy leaf area, and more dependent on the coupling between canopy conductance and atmospheric humidity. Whitehead and Jarvis (1981) related the degree of coupling in a forest canopy to the functional relationship between leaf area and sapwood area. Thus, biomass partitioning between water supply and water use structures in forest trees at the field site, may be important on temporal scales relevent to the life of the trees (10^1 - 10^2 years), rather than at the time scale relevent to maximum daytime transpiration rates.

In general, despite large variation in stomatal conductances between different species, transpiration rates from forest canopies vary within a limited range, irrespective of forest species composition, stand age and canopy structure (Dunin and Mackay 1982; Roberts 1983; Whitehead 1985; Shuttleworth 1989). Additionally, these transpiration rates are less than two-thirds the potential evaporation of a freely evaporating surface at temperate latitudes, but up to 0.8 - 0.9 potential evporation in tropical forests (Doley 1981). Maximum forest transpiration rates tend to fall between 0.1 and 0.5 mm h^{-1} regardless of species and forest type (McNaughton and Jarvis 1983). These values correspond to 1.5 - 7.7 mmol m^{-2} s^{-1}. This limitation on transpiration is due to the relationship between canopy conductance and saturation deficit (Figs. 5.12 and 5.14).

Increasing saturation deficit potentially increases transpiration, as indicated by the proportionality between transpiration and saturation deficit in equation 5.8. However, the negative relationship between saturation deficit and canopy conductance may either limit the increase, maintain constant or even decrease transpiration rates with increase in evaporative demand. The sensitivity of stomatal conductance to humidity is indicated by the slope of the saturation deficit/canopy conductance relationship (Roberts 1983). Large reductions in conductance for a given change in saturation deficit, indicate greater sensitivity of stomata to a change in humidity. Whitehead *et al.* (1984) suggested that, for conifers, greater stomatal sensitivity is characteristic of species from maritime or humid climates, whereas lower sensitivity is a characteristic of species from arid climates. However, data from both the present work and other studies do not support this idea (Fig. 6.5). Stomatal sensitivity to humidity in canopy studies varied between forest types despite annual precipitation greater than 1000 mm in all cases (Fig. 6.5). Thus, variation in average canopy stomatal sensitivity to changes in water vapour may vary between species and forest types independent of regional climate. However, greater conductance to water vapour at high humidities may contribute to high rates of photosynthesis. For example, Unwin and Kriedemann (1990) suggested that greater incremental increases in stem cross-sectional area in *Acacia aulacocarpa* and *Melia azederach* on coastal, more humid sites in northern Queensland, was due to the reduced cost of assimilation at lower leaf to air vapour pressure differences.

In the present study, the relationship between humidity and mean maximum canopy conductance to water vapour per unit leaf area was similar in rainforest and eucalypt forest plots (Fig. 5.14). Thus, despite considerable differences in canopy structure averaged over the whole canopy (Chapter 3), similar transpiration rates per unit leaf area would be expected for a given humidity. These results concur with other reports indicating similar canopy transpiration rates despite variation in forest composition and canopy structure (Roberts 1983; Whitehead *et al.* 1984; Whitehead 1985). Equivalent transpiration rates between different forest types are due to close coupling between

transpiration, conductance to water vapour and atmospheric humidity (McNaughton and Jarvis 1983 and 1991; Jarvis and McNaughton 1986). At the gully bottom, maximum canopy conductance per unit crown area was greater than on other plots in winter and autumn (Fig. 6.5a), presumably due to greater water availability. High canopy conductances per unit crown area produced higher transpiration rates in winter and autumn (Fig 5.11). However, maximum transpiration rates remained high during summer even though canopy conductance declined. This was attributed to a higher leaf area index and greater interception of radiation by more horizontally orientated leaves contributing to an increased canopy to air vapour pressure difference (Figs 5.6 - 5.8).

The third hypothesis (Chapter 1) proposed that canopy transpiration and conductance to water vapour would differ between rainforest and eucalypt forest. Eucalypt trees were expected to display water conservative characteristics, in contrast to rainforest trees. The results presented in Chapter 5 suggest that average leaf conductances to water vapour were similar between rainforest and eucalypt forest plots (Fig. 5.14). Similar responses between species to humidity may be due to the strong coupling between regional humidity and stomatal responses to the relatively humid regional climate of southeastern New South Wales.

Summary

In conclusion, plant growth and water use characteristics were studied in rainforest and eucalypt species from southeastern New South Wales, Australia. Species differences in responses to variation in microenvironments associated with aspect can be related to differences in the distribution of rainforest and eucalypt species. The aim of this chapter was to integrate experimental results from preceeding chapters and other studies into a conceptual model of processes governing the differential distribution of different vegetation types with aspect.

The inference drawn from glasshouse experiments is that higher biomass under experimental treatments may result in enhanced growth and survival by seedlings in the field. Thus, even though both rainforest and eucalypt forest species grew under all light and water treatments, vegetation distribution in the field is controlled by processes which exclude eucalypts from rainforest and vice-versa. That eucalypt species do not establish beneath rainforest canopies is established (eg. Ashton 1981b; Unwin 1989a). The question critical to the conceptual model proposed in Fig. 6.1, is what processes prevent establishment of rainforest in eucalypt forest? Consideration of the role of fire alone suggests that, should fire be eliminated from a given site, rainforest will establish and eventually exclude eucalypt forest. However, results from glasshouse experiments indicate traits possesed by rainforest species, such as slow growth rates and shallow root systems, which may be detrimental to survival on exposed aspects. Such traits may limit rainforest distribution to more mesic sites during periods of severe drought irrespective of fire frequency and intensity. Furthermore, observations such as yellowing of leaves by rainforest species and the downward trend in mean plant biomass with an increase in irradiance from 21-42% to 65-88% in both *C. apetalum* and *D. sassafras* (Fig 2.4), may indicate underlying physiological processes, such as photoinhibition of photosynthesis (see Powles 1984), which may contribute to lower survival by rainforest species on exposed aspects. Processes restricting rainforest establishment on exposed aspects may be investigated in future by reciprocal transplant experiments, where rainforest and eucalypt forest species are transplanted onto exposed and sheltered aspects under different light and water treatments. The results from such an experiment would contribute toward a mechanistic understanding of processes controlling vegetation distribution.

The principal findings of the thesis in the context of rainforest and eucalypt forest distribution are:

(1) Variation in light was the principal determinant of plant biomass in pot grown juveniles of rainforest and eucalypt forest species, rather than soil moisture content and nutrient availability. Higher growth rates were produced at high light, water and nutrient treatments in eucalypt species which naturally occur on ridge tops and exposed aspects. Higher growth rates were produced under low irradiance in rainforest species which naturally occur on sheltered aspects and at the gully bottom.

(2) Morphological plasticity in response to different light levels, was greater in eucalypt species characteristic of high light environments. This plasticity may be an important mechanism by which eucalypt species acquire resources to achieve high rates of growth. However, growth rates in eucalypts decline under irradiances less than 20% sunlight despite their morphological plasticity.

(3) Partitioning of biomass to roots may increase water availability under high irradiance, thereby maintaining transpiration rates. Under high irradiance and low soil moisture, rapid root growth and more ramified root systems in eucalypts may maintain water supply to leaves at high evaporative demand. Slower root growth in rainforest species may restrict access to water, thereby limiting growth and increasing the probability of seedling mortality on dry, exposed sites.

(4) Transpiration rates in canopy trees are determined by physical and physiological processes governing evaporative demand, water supply and the control of water vapour loss from the canopy. However, transpiration rates are independent of soil moisture content in the upper surface layers, presumably because canopy trees obtain water from deeper soil layers. Lateral sub-surface drainage may increase water availability at the gully bottom, and exploitation of this water may contribute to high conductances per unit crown area. Lower conductances in canopy trees on slopes above the gully bottom may be due to lower water availability. On these slopes, less sapwood area per unit sap

flow in eucalypts may indicate lower internal resistance to water transport, and be an adaptation to restricted water availability.

(5) Regional climate, mediated by aspect and topography, in conjunction with water availability below soil surface layers, may define environmental limits which determine the maximum foliage area index in any location. Plant growth within these environmentally imposed limits may be closely tied to observed vegetation distribution patterns in southeastern New South Wales.

(6) Fire is an integral part of Australian ecosystems. However, it is not an external control of vegetation distribution, independent of biological and physical processes. Fire may be important in determining the sharpness of the ecotone between rainforest and eucalypt forests and, in association with plant physiological responses to microenvironment, may limit rainforest establishment on exposed aspects. However, if fire were completely excluded from the ecosystem, rainforest communities may remain excluded from exposed aspects and ridge tops by environmental limits on plant growth and survival.

(7) The distribution of rainforest and eucalypt vegetation in eastern temperate Australia may be controlled at the regional scale by climatic influences, such as precipitation and humidity, and at the catchment scale by aspect mediation of microclimate in association with the feedback of the canopy on both microenvironment and fire behaviour. Both feedback processes may reinforce and stabilise rainforest and eucalypt vegetation distribution patterns on exposed and sheltered aspects in eastern temperate Australia.

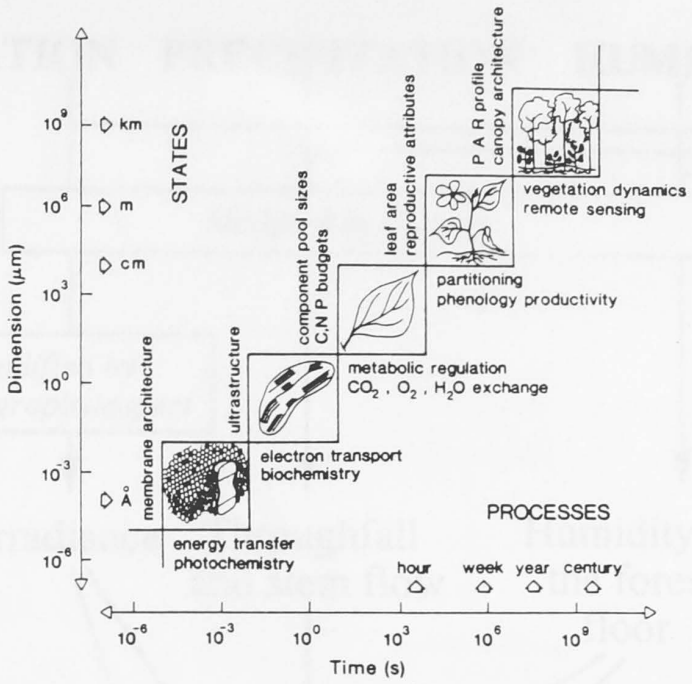


Figure 6.1. Schematic representation of the spatial and temporal scale of biological processes reproduced from Osmond and Chow (1988). The axes represent the time taken for each arbitrary level of complexity to return to equilibrium after perturbation and the approximate spatial scale (in μm) over which processes operate.

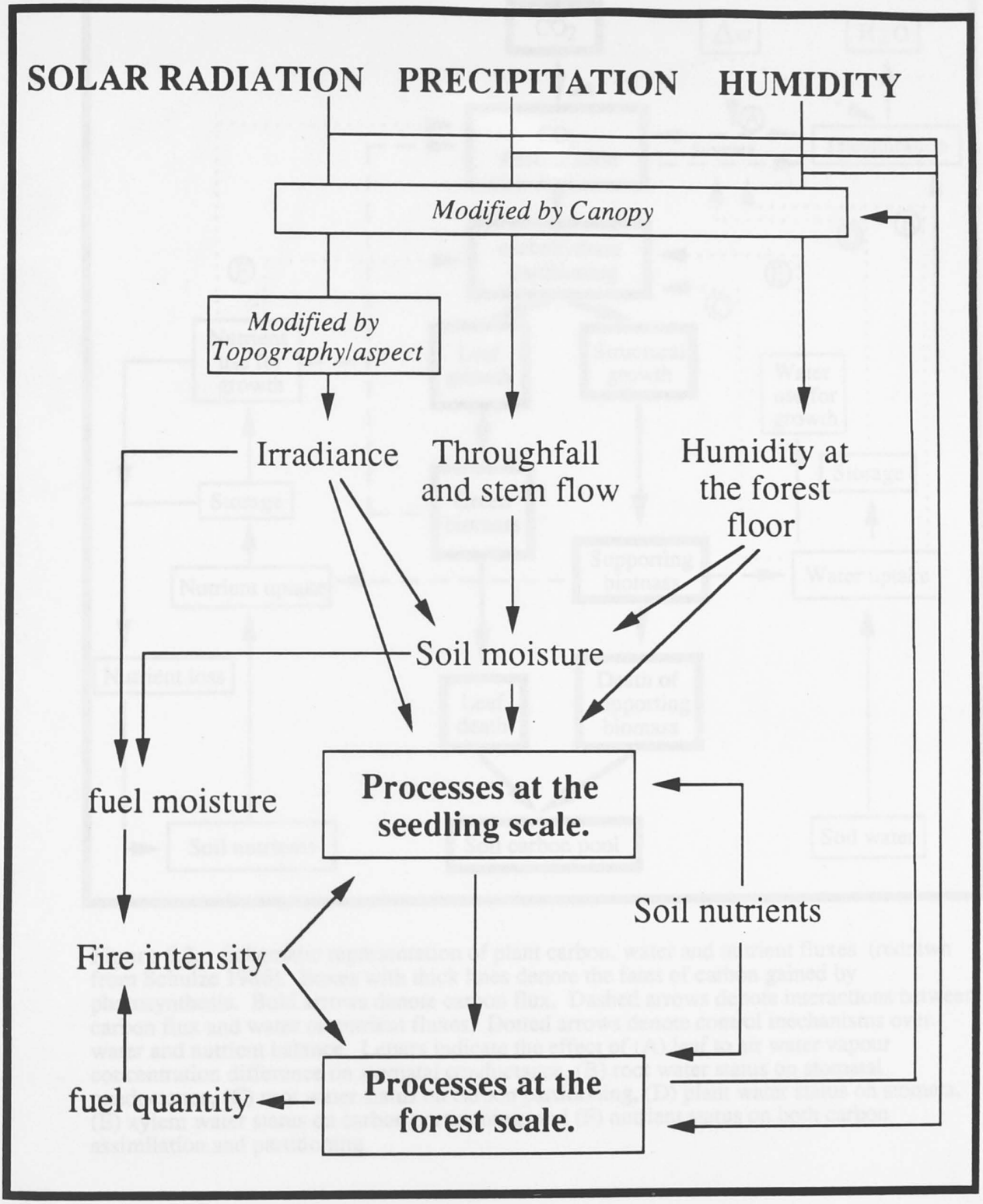


Figure 6.2. A conceptual model outlining the relationships between physical and biological processes at the catchment scale which may determine the differential distribution of rainforest and eucalypt forest throughout eastern temperate Australia. Arrows imply a causal effect. Processes of growth, biomass partitioning and water use characteristics at the seedling and forest scale are discussed in the text.

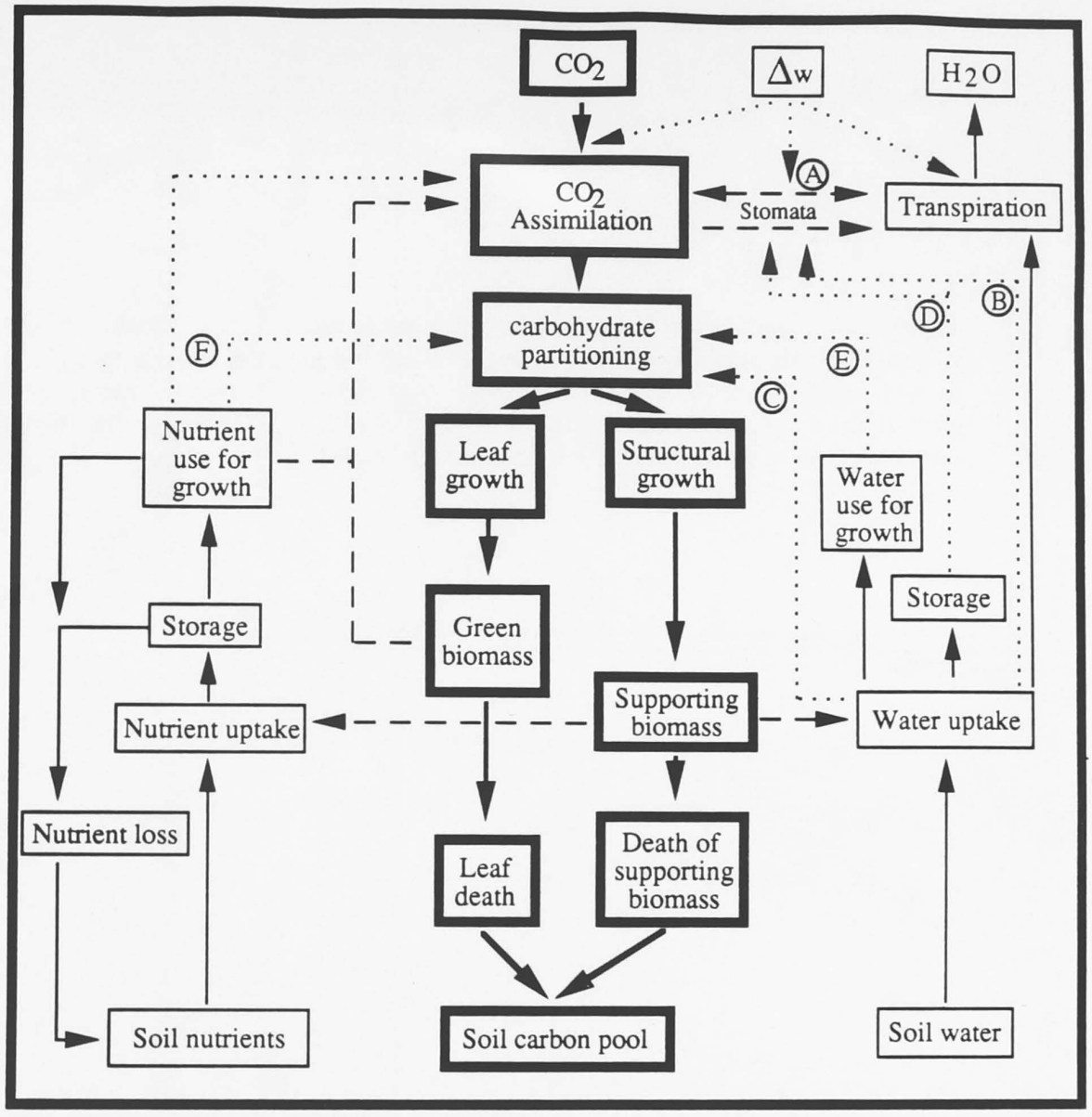
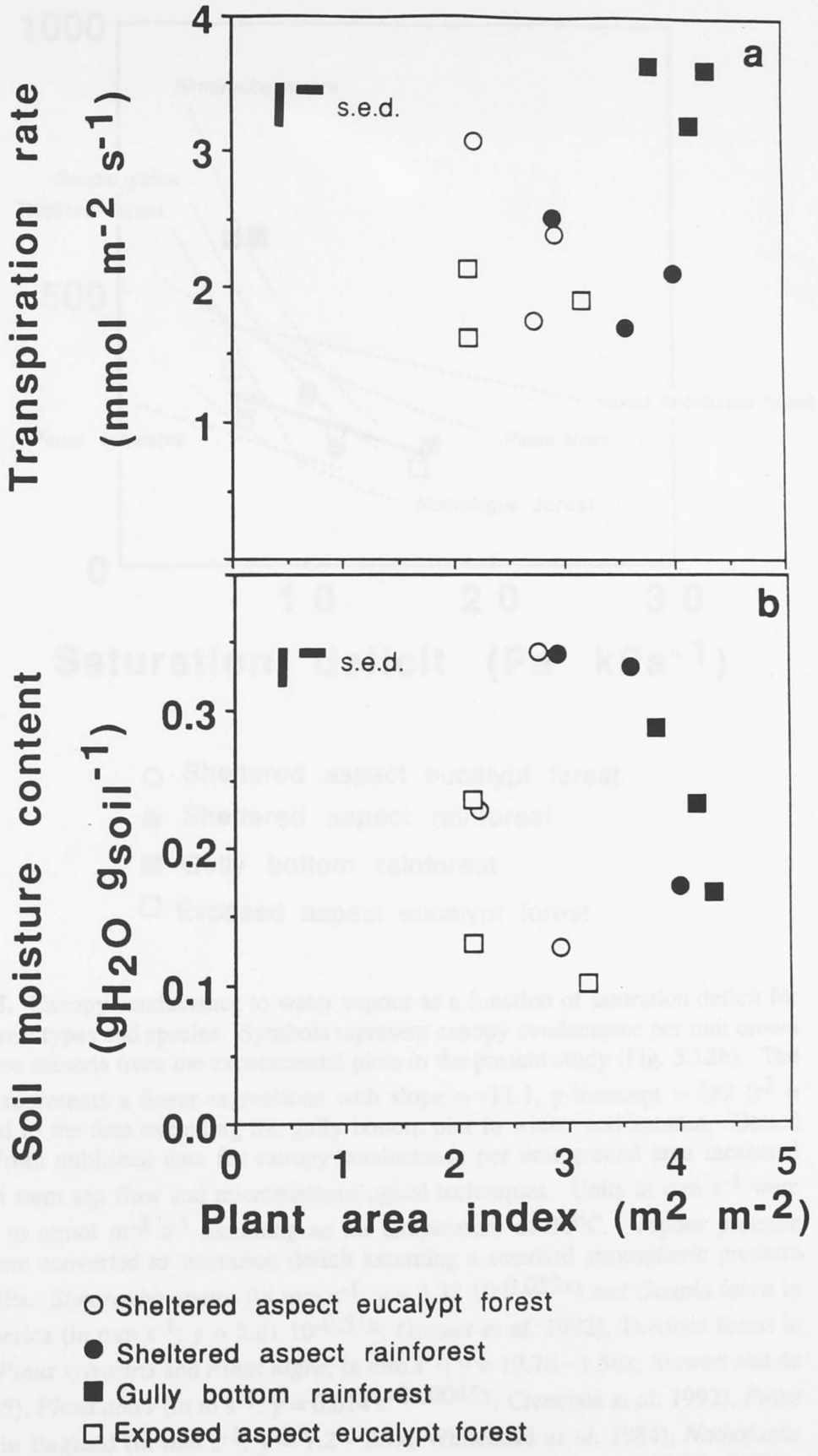


Figure 6.3. Schematic representation of plant carbon, water and nutrient fluxes (redrawn from Schulze 1986). Boxes with thick lines denote the fates of carbon gained by photosynthesis. Bold arrows denote carbon flux. Dashed arrows denote interactions between carbon flux and water or nutrient fluxes. Dotted arrows denote control mechanisms over water and nutrient balance. Letters indicate the effect of (A) leaf to air water vapour concentration difference on stomatal conductance, (B) root water status on stomatal conductance, (C) root water status on carbon partitioning, (D) plant water status on stomata, (E) xylem water status on carbon partitioning, and (F) nutrient status on both carbon assimilation and partitioning.

Figure 6.4. Relationship between plant area index and (a) mean maximum canopy transpiration rate per unit crown area, and (b) mean soil moisture content above 0.35 m, in four experimental plots at the field site. Transpiration and plant area index data derived from means of eight trees per plot. Vertical and horizontal bars represent standard errors of the difference of mean for each variate.


a
s.e.d.
Transpiration rate
(mmol m-2 s-1)
4
3
2
1
b
s.e.d.
Soil moisture content
(gH2O gsoil-1)
0.3
0.2
0.1
0.0
0
1
2
3
4
5
Plant area index (m2 m-2)
Sheltered aspect eucalypt forest
Sheltered aspect rainforest
Gully bottom rainforest
Exposed aspect eucalypt forest

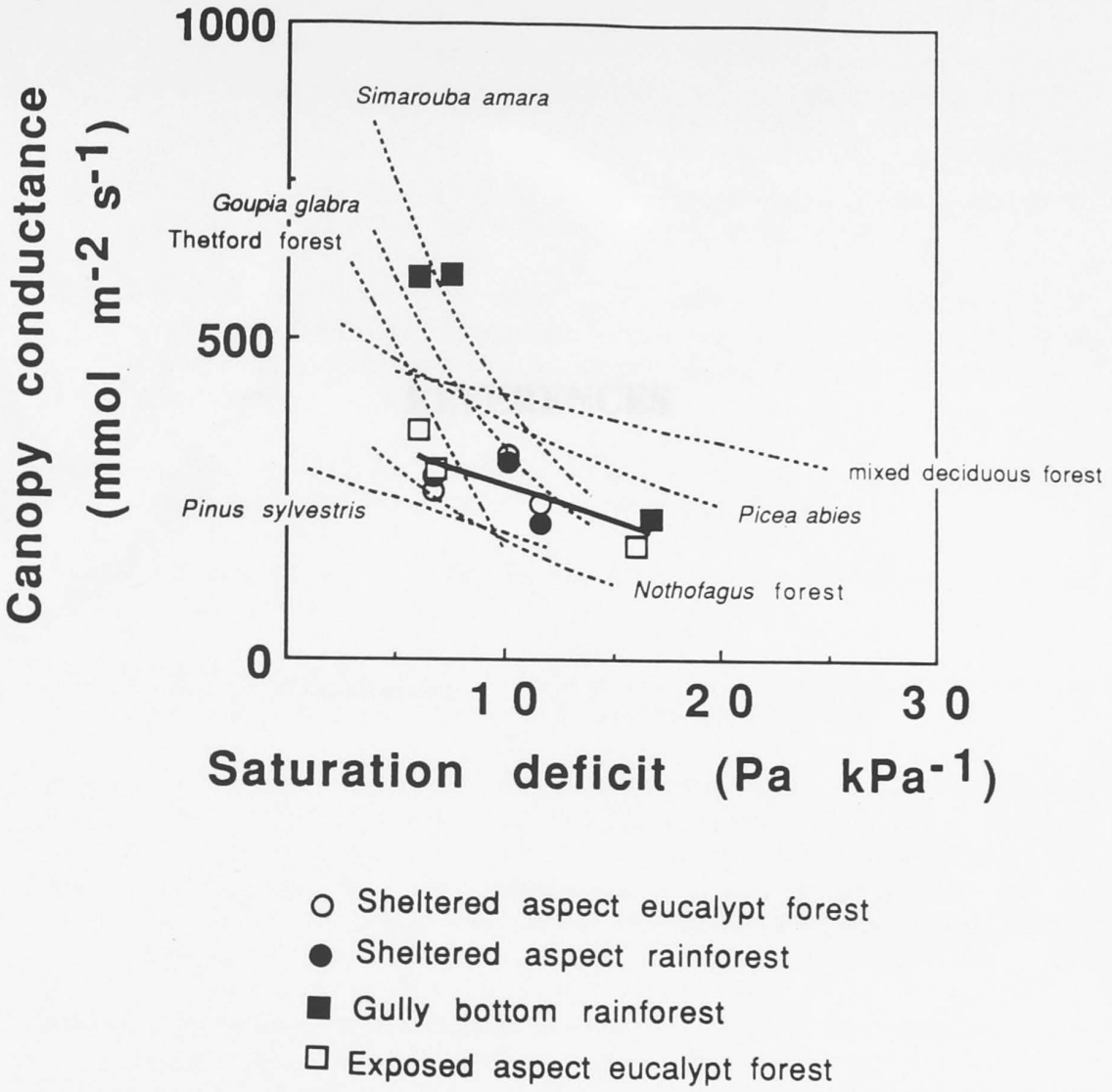


Figure 6.5. Canopy conductance to water vapour as a function of saturation deficit for various forest types and species. Symbols represent canopy conductance per unit crown area in three seasons from the experimental plots in the present study (Fig. 5.12b). The solid line represents a linear regressions with slope = -11.1, y-intercept = 382 (r^2 = 0.58) fitted to the data excluding the gully bottom plot in winter and autumn. Dotted lines are from published data for canopy conductance per unit ground area measured using both stem sap flow and micrometeorological techniques. Units in mm s^{-1} were converted to mmol m^{-2} s^{-1} assuming an air temperature of 20°C. Vapour pressure deficits were converted to saturation deficit assuming a standard atmospheric pressure of 101.3 kPa. *Simarouba amara* (in mm s^{-1}; $y = 3.32\ 10^{-0.052x}$) and *Goupia labra* in South America (in mm s^{-1}; $y = 2.61\ 10^{-0.51x}$; Granier *et al.* 1992), Thetford forest in England (*Pinus sylvestris* and *Pinus nigra*; in mm s^{-1}; y = 19.76 - 1.56x; Stewart and de Bruin 1985), *Picea abies* (in m s^{-1}; $y = 0.014\ e^{-0.00045x}$; Cienciala *et al.* 1992), *Pinus sylvestris* in England (in mm s^{-1}; y = 7.2 - 2.7x; Whitehead *et al.* 1984), *Nothofagus* forest in New Zealand (*Nothofagus fusca, N. menziesii*; in mm s^{-1}; $y = e^{(2.45 - 1.71x)}$; Kostner *et al.* 1992), mixed deciduous forest in North America (*Acer sacharinum, A. rubrum, Alnus rugosa, Betula papyrifera, Fraxinus nigra, Ulmus americana* and *Thuja occidentalis*; in mm s^{-1}; y = 11.85 - 1.8x; Munro 1989).

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